

CARBON AND NITROGEN UPTAKE DYNAMICS DURING 1997 AND 1998
ANOMALOUS CONDITIONS IN THE BERING SEA

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**CARBON AND NITROGEN UPTAKE DYNAMICS DURING 1997 AND 1998
ANOMALOUS CONDITIONS IN THE BERING SEA**

A

THESIS

**Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of**

MASTER OF SCIENCE

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Fairbanks, Alaska

December 2000

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ABSTRACT

During 1997 and 1998, unusual physical conditions caused dramatic changes in the regional oceanic environment and function of the southeastern Bering Sea ecosystem. The changes in ecosystem function were examined using ^{13}C and ^{15}N tracer techniques. In 1997, unusually clear and calm conditions allowed an ice-related early bloom over the middle shelf of the southeastern Bering Sea and resulted in nitrate uptake below the pycnocline. In 1998, the duration of phytoplankton growth was extended by warm temperatures and frequent storms that resulted in slow growth of phytoplankton and prevented rapid utilization of nitrate over the shelf. In coccolithophorid bloom regions, ammonium concentrations were high ($>3\ \mu\text{M}$), while nitrate concentrations had a larger range ($0.1\text{-}10.8\ \mu\text{M}$). Nitrate utilization rates, which estimate "new" production, were similar for both years and were somewhat greater (ca. 30%) than those observed during the 70's and 80's PROBES studies. The fate of primary production may have differed in 1997 and 1998.

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ACKNOWLEDGEMENTS

Thanks to God for bringing me to Fairbanks and giving me a chance to study the Bering Sea shelf. I owe great thanks to my graduate committee, Donald Schell and Susan Henrichs, for their time spent answering my many questions and their valuable comments on this thesis. Dr. Dean Stockwell provided valuable discussions relating to data analysis. I'm really grateful to Dr. Terry Whitledge for his extensive mentoring. I met him at first on Miller Freeman cruise in May 1997. After he moved to Fairbanks, he provided me with many of his priceless time for discussions about data processing and polishing my poor English writing. Special thanks to Dr. John Goering, as my major advisor, for everything he gave me from academic knowledge to financial support. His comfortable personality allowed me to bring very simple questions to him.

I acknowledge the endurance of my wife Kyung Sook and my children Si Young and Ji Hyun. I was not always available when they needed me. Without their patience, I could not have accomplished the research and writing of this thesis. I would also like to acknowledge the support of my parents, brother, sister-in-law, and parents-in-law.

This work was supported by the NOAA-funded Southeast Bering Sea Carrying Capacity (SEBSCC) ecosystem project, the NOAA-UAF Cooperative Institute For Arctic Research (CIFAR) funded primary productivity study, and the NSF-funded Inner Shelf Front (IF) study.

1. INTRODUCTION

1.1 Importance of new production in understanding recent biological productivity trends on the Bering Sea shelf

The Bering Sea Shelf is one of the most productive areas in the world ocean. It provides a major portion of the total world fishery catch, although it covers only 0.33% of the world's ocean area (Goering and McRoy, 1981). This harvest is comparable to the shelves off Nova Scotia and the northern North Sea in terms of the catch per unit area (Coachman and Walsh, 1981). In the 1990s, the Bering Sea ecosystem received even more attention after the collapse of the U.S. fishery on the New England continental shelf (NRC, 1996). There have recently been noticeable declines in the abundance of several species of marine mammals (e.g., sea lions, fur seals and sea otters) and sea birds (common murres, thick billed murres, and red- and black-legged kittiwakes) (NRC, 1996). These declines coincide with fluctuations in fish stocks recently reported for the southeastern Bering Sea Shelf.

Primary production is a very important factor in understanding the changes recently observed in the southeastern Bering Sea shelf ecosystem. Walsh and McRoy (1986) found that interannual variation in year class strength of Alaskan pollock was related to the food availability during their larval stage. Lasker (1975) reported that subsurface chlorophyll-a maxima were very important for larval fish survival. Subsurface chlorophyll-a maxima were also related to the survival of juvenile pollock in the southeastern Bering Sea shelf region (Nishiyama *et al.*, 1982).

Dugdale and Goering (1967) divided primary production into "new" and "regenerated" production based on the nitrogen source. "New" production is the

proportion of primary production in a euphotic zone associated with all external nitrogen input from deep water (nitrate), atmosphere (nitrogen fixation), precipitation, or river discharge. "Regenerated" production is that which is based upon the internally recycled nitrogen (ammonium and urea) within the euphotic zone. The export of organic nitrogen from a system should balance the uptake of external nitrogen if the production system is to be maintained at a steady state. Thus, "new" production would correspond to the flux of organic matter from the euphotic layer as sinking particles to the deeper water or higher trophic levels (Eppley and Peterson, 1979).

1.2 Southeastern Bering Sea shelf

The southeastern Bering Sea shelf can be divided into three distinct areas - inner, middle, and outer shelf. Each area is separated by distinct frontal systems, which result in unique characteristics of hydrography and biological and chemical processes within each domain (Coachman, 1986; Kinder and Coachman, 1978; Schumacher *et al.*, 1979). The inner shelf is located between the Alaskan mainland and the 50 m isobath. The water column is homogeneous due to the overlapping of tidal and wind mixing energy within the shallow water column. In the middle shelf (between the 50 m and 100 m isobaths), during the spring and summer season, a strong pycnocline develops and separates the water column into two distinct reservoirs, with a wind-driven surface mixed layer and a tidally-driven lower mixed layer. Generally, it is believed that the introduction of buoyancy (e.g. ice melt and solar heating) is responsible for the development of a two-layered water column in the middle shelf region. Mooring data suggest that in some years both ice and advection of relatively warm, saline water at depth are important mechanisms that stratify the water column (Stabeno *et al.*, 1998). In the outer shelf (100 m- 200 m), a three-layer water column is typical. A fine structure separates the wind

mixed layer from the tidally mixed lower layer. The formation of fine structure in water mass properties between the upper and lower homogeneous layer is distinctive and critical in the distribution of properties in the water column, both horizontally and vertically (Coachman, 1986).

Over the southeastern Bering Sea shelf, water motion can be divided into high frequency tidal currents and lower frequency flows. Tidal currents provide major amounts of the horizontal kinetic energy over the entire shelf region: ~ 80% at the outer shelf, ~ 100% at the middle shelf, and ~ 95% at the inner shelf (Coachman, 1986). They also generate sub-tidal flows by non-linear interactions between tidal currents and bottom topography (Kowalik, 1999). Low frequency currents (Fig. 1) are also evident from a synthesis of direct observation data with moorings, satellite-tracked drifting buoys, and hydrographic sections (Schumacher and Stabeno, 1998). In the inner shelf region, there is a significant counterclockwise mean flow ($1-6 \text{ cm s}^{-1}$) along the 50-m isobath. The main source of this current is the Alaska Coastal Current, which enters the Bering Sea through Unimak Pass and is reinforced by freshwater additions (Schumacher and Stabeno, 1998; Schumacher *et al.*, 1979; Reed and Stabeno, 1996). Limited numbers of current records have been collected over the middle shelf and away from the boundaries with adjacent regions. These data show that there are large fluctuations of subtidal currents with short duration (several days) in the middle shelf region, although overall flow is weak (Stabeno *et al.*, 1998). A weak cross-shelf flow north of the Pribilof Islands transports nutrient rich slope water into the inner shelf region (Stabeno *et al.*, 2000). In the outer shelf, there is a mean flow of $4-8 \text{ cm s}^{-1}$. Some of this flow ($1-5 \text{ cm s}^{-1}$) enters the Bering Sea through Unimak Pass and follows the 100-m isobath toward

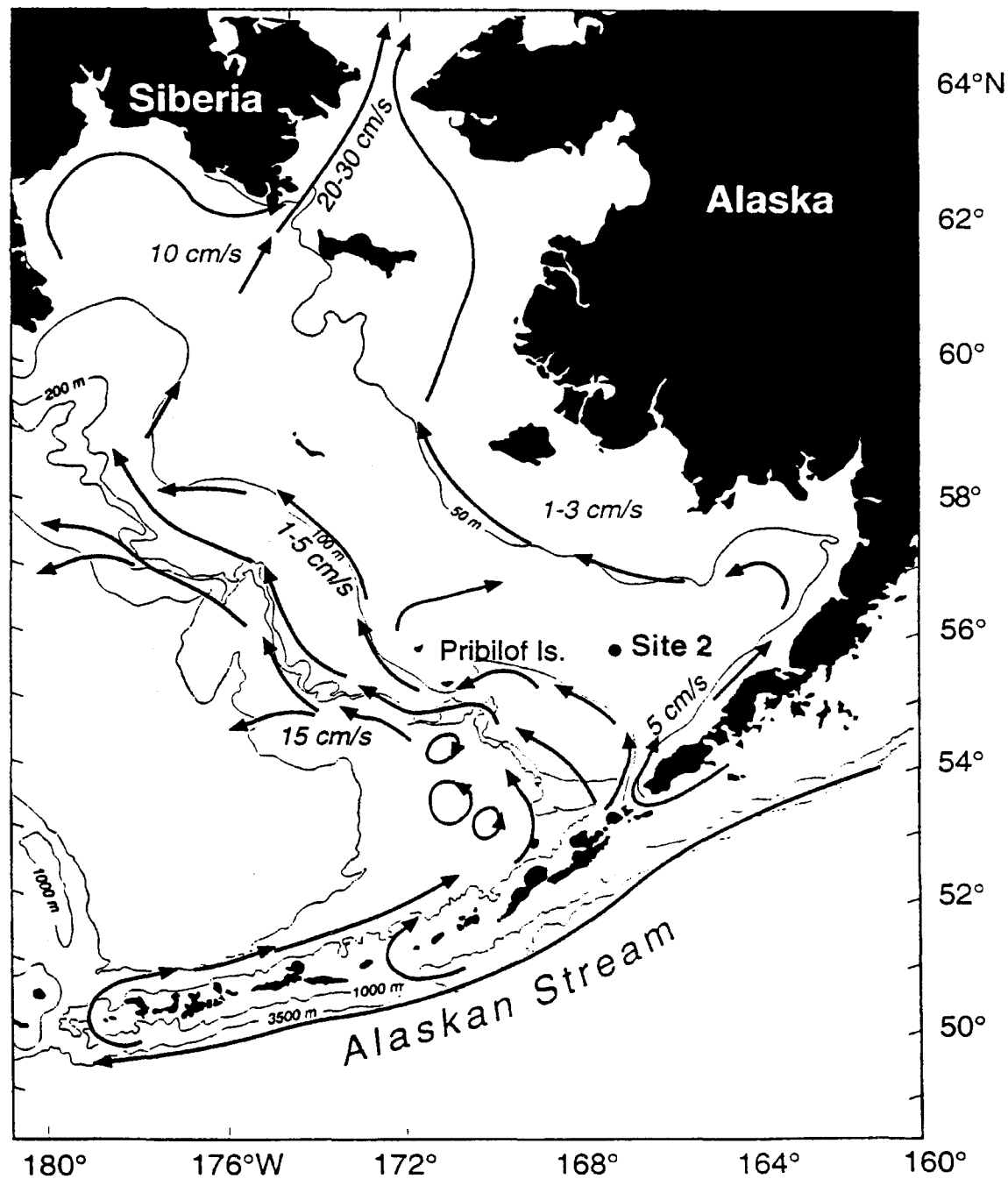


Fig. 1 A schematic of flow on the eastern shelf in the upper 40m of the water column generated from a synthesis of moored current meters, satellite-tracked drift buoys and inferred geostrophic flow. Depths are in meters. (After Schumacher and Stabeno, 1998; Stabeno et al., 1999).

the northwest (Coachman, 1986; Schumacher and Stabeno, 1998). There are also strong flows ($> 10 \text{ cm s}^{-1}$) over the shelf break (Schumacher and Reed, 1992) and significant onshelf-offshelf mean flows of $1\text{-}5 \text{ cm s}^{-1}$ with durations of a few days (Coachman, 1986).

The southeastern Bering Sea shelf region is relatively shallow and a large proportion of the shelf area experiences a seasonal advance and retreat of sea ice. It is also well known that primary production over the southeastern Bering Sea shelf is influenced by the seasonal ice arrival and retreat in early spring (Alexander and Niebauer, 1981; Niebauer and Alexander, 1985; Niebauer *et al.*, 1990; Stabeno *et al.*, 2000). As seasonal sea ice retreats, the melting provides cold and low salinity water to the initially high nutrient water and forms strong stratification and a shallow surface wind mixed layer. This initiates a phytoplankton bloom along the ice edge. In most years, the ice edge bloom is short lived due to open water column wind mixing and the rapid consumption of nitrate by phytoplankton. After the spring storms bring nutrients into the surface layer, the more typical water column spring bloom occurs in late April-early May (Niebauer *et al.*, 1990). Under ice phytoplankton blooms in the absence of stratification have also been observed (Stabeno *et al.*, 1998). In 1995, spring storms were not energetic enough to replace nitrate consumed during the under ice bloom. Thus the under ice bloom was the only phytoplankton bloom that spring. Therefore, the advance and retreat of seasonal sea ice can greatly affect the seasonal distribution of the total annual primary production over the Bering Sea shelf, through the occurrence of the ice edge related phytoplankton bloom.

Large calanoid copepods and euphausiids (*Neocalanus plumchrus*, *N. cristatus*, *Eucalanus bungii*, *Thysanoessa inermis* and *Thysanoessa raschii*) are major

zooplankton species in the outer shelf (Cooney and Coyle, 1982). The large herbivores exclusively graze diatoms, which results in a phytoplankton community dominated at times by *Phaeocystis poucheti* (Iverson *et al.*, 1979). Therefore, most of the primary production by diatoms is efficiently transferred to the pelagic food web (Goering and McRoy, 1981). In the middle shelf, diatoms contribute most of the spring productivity and show a succession of dominant species from small sizes (*Thalassosira* and *Chaetoceros*) to medium sizes (*Chaetoceros*, *Corethron*, and *Nitzschia*) and a large, long chained variety (*Rhizosolenia alata*), due to changing conditions in the water column. The presence of large copepods is constrained to the outer shelf by physical barriers, such as the middle front. Small copepods (e.g., *Pseudocalanus spp.*, *Oithona similis*, *Acartia longiremis*) are distributed across the entire shelf. The small copepods of the middle shelf reproduce several times per year following the spring phytoplankton bloom. *C. marshallae* often only has a single cohort, but in warm years may have a second cohort during the summer (Smith and Vidal, 1986). Therefore, significant fractions of primary production escape grazing by herbivores and are utilized by the benthic food web (Goering and McRoy, 1981). These differential grazing activities on the southeastern Bering Sea shelf are evidenced in the large stocks of birds, mammals, and pelagic fish (primarily walleye pollock) in the outer shelf and the large stocks of benthic infauna, demersal fish, and crabs in the middle shelf (Iverson *et al.*, 1979).

During the late 70's and early 80's PROBES project, there were extensive studies of the relationship between physical conditions, especially wind mixing, and development of the spring phytoplankton bloom in the southeastern Bering Sea shelf (Sambrotto *et al.*, 1986). Primary production over the middle shelf depended on the amount of nutrients, especially nitrate concentrations, in the surface euphotic layer.

Diatoms were the dominant phytoplankton group during the spring bloom in this region (Iverson *et al.*, 1979). Ammonium was the more favorable nitrogen source for phytoplankton. Nitrate, however, supported over half the nitrogen uptake for phytoplankton during the spring bloom in the southeastern Bering Sea shelf (Dagg *et al.*, 1979). Nitrate concentrations reached a maximum before the phytoplankton bloom and were depleted from the upper 40m surface layer during the bloom. Intermittent storm events during the summer can break the strong stratification and mix high nutrient deep water into the nutrient depleted surface layer. Continued high post spring bloom nitrate uptake rates over the middle shelf accounted for up to 37% of annual "new" production during 1980 and 1981 (Sambrotto *et al.*, 1986).

There have been several measurements of primary production made over the southeastern Bering Sea shelf (Table. 1). In the inner shelf area, total primary production ranges from 50 to 100 g C m⁻² y⁻¹ and "new" production is less than 20 g C m⁻² y⁻¹, due to the slow renewal and small initial inventory of nutrients (Hansell *et al.*, 1993; Springer and McRoy, 1993). Over the middle shelf, production is greater than in the inner shelf due to the larger initial nutrient inventory (NRC, 1996). Total primary production ranges from 150-200 g C m⁻² y⁻¹ and "new" production from 30-50 g C m⁻² y⁻¹ (Hansell *et al.*, 1993). In the outer shelf, total production is about 200 to 250 g C m⁻² y⁻¹ and "new" production ranges from 40 to 70 g C m⁻² y⁻¹ (Hansell *et al.*, 1993).

1.3 Changing conditions over the southeastern Bering Sea shelf

The southeastern Bering Sea shelf experienced large changes in physical and biological conditions during the last decade. During the Processes and Resources of the Bering Sea Shelf (PROBES) late 1970's and early 1980's studies, sea ice did not cover mooring 2 (M2) in the middle shelf area, studied during the Southeastern Bering Sea

Table 1. Existing estimates of total production over the southeastern Bering Sea shelf.

Source	Production (g C m ⁻²)	Method	Comments
Hansell et al., 1993	30-50 40-70	NO ₃ ⁻ disappearance	Middle shelf; July 1983 Outer shelf, July 1983
Whitledge et al., 1986	53 39	NO ₃ ⁻ disappearance	Middle shelf; 31 day spring period, mean for 1979-1981. Uncorrected for diffusive resupply of nitrate Outer shelf; 31 day spring period, mean for 1979-1981. Uncorrected for diffusive resupply of nitrate
Sambrotto et al., 1986	66 48 35	¹⁵ NO ₃ ⁻ uptake	Station 12; 1979 Station 12; 1980 Station 12; 1981 Station 12 is in the middle shelf; calculated assuming a C:N uptake ratio of 6 by atoms
Codispoti et al., 1986	100 60	total CO ₂ decrease	1980; middle shelf 1981; middle shelf
Taguchi, 1972	55	¹⁴ C uptake	June 1968; based on three shelf stations and assuming a 120 day growing season.

Carrying Capacity (SEBSCC) 1997 and 1998 project. Hence, there was no local ice-related blooms near the mooring 2 (M2) site. After early 1990s, sea ice appeared more often in this region, and the duration and extent of sea ice showed interannual variations. The variations of the extent, timing, and persistence of sea ice cover and atmospheric conditions affect the timing and location of primary production and its transfer through the food web (Niebauer *et al.*, 1990; Stabeno *et al.*, 1998). Wyllie-Echeverria and Ohtani (1999) report that sea ice extent in the Bering Sea has interannual and multi-annual variations. These variations have different effects on the populations of fish, birds, and mammals on the shelf. Hare and Mantua (in press) have analyzed 100 physical and biological data series, which suggest that there were two distinctive regime shifts during the 1965 -1997 period: a 1976-1977 shift and a 1988-1989 shift. In the 1989 regime shift, signals are more evident in biological records than in indices of Pacific climate. However, the temporal variability of spatial patterns of sea ice over the middle shelf (Fig. 2) generally coincides with the regime shift and /or interdecadal climate variations (Stabeno *et al.*, 1999). From 1972-1976 there was a cold period, from 1977-1988 a warm period, and from 1989-1998 a weaker cold period.

The Bering Sea Shelf is also highly sensitive to meteorological and climatological forcing (i.e., local radiative warming and cooling, thermal advection, wind mixing, and storm activity). Climate can modify the Bering Sea shelf ecosystem dynamics through changes in the timing and the location of nutrient inputs, as well as the response of individual phytoplankton species to physical forcing (Stabeno *et al.*, 1998). Springer (1998) suggests that fluctuations of physical forcing are responsible for the variability in higher trophic levels, such as sea birds and mammals, through changes in food web

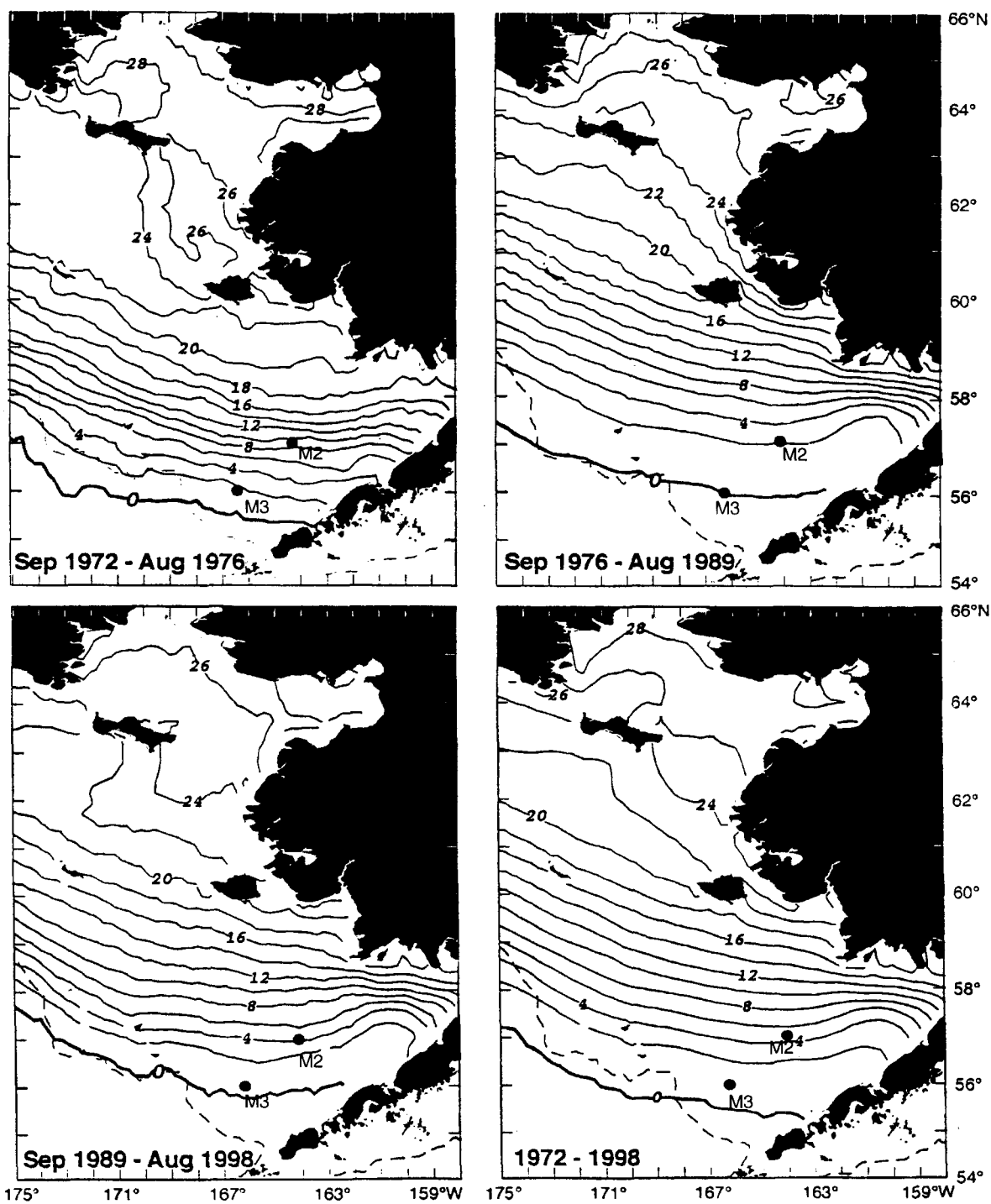


Fig. 2 Contours of the number of weeks that sea ice was present over the southeastern Bering Sea shelf. The average ice coverage during (a) 1972-1976, (b) 1977-1988, (c) 1989-1998, and (d) 1972-1998 (from Stabeno *et al.*, 2000).

dynamics. Wind-driven advection of surface water may be responsible for the fluctuations in year-class strength of pollock (Wespestad *et al.*, 2000) and Tanner crabs (Rosenkranz *et al.*, 1998).

During 1997 and 1998, the southeastern Bering Sea shelf experienced very unusual atmospheric conditions. In 1997, ice cover did not differ greatly from average, yet the northward retreat of sea ice was rapid, cloud cover was diminished, and storm events were infrequent, which resulted in the warmest sea surface temperature ever observed and a low water column heat content (Stabeno *et al.*, 2000). In 1998, storm events were more frequent than usual, allowing a weak pycnocline to develop for only short periods of time. The high heat content of the water column resulted from the absence of sea ice and northerly winds. The surface mixed layer often extended to about 70-m water depth. Nitrate inventories below the pycnocline were depleted during 1997. During 1998, the water column heat content was higher than in 1997 although surface water temperatures were cooler (Stabeno *et al.*, 2000). A coccolithophorid bloom occurred in early July 1997 and re-occurred in 1998. In addition, a massive die-off of shearwaters was reported during 1997 and salmon returns to Bristol Bay were lower than predicted during both 1997 and 1998. Wind mixing events were much more frequent in 1998 than in 1997 (Vance *et al.*, 1998; Hunt *et al.*, 1999; Stockwell *et al.*, submitted).

1.4 Study objectives

Sambrotto *et al.* (1986) conducted detailed research on nitrogen uptake rates in conjunction with physical conditions over the southeastern Bering Sea shelf, but the climate regime during their study was quite different from the present. As mentioned earlier, large variations in physical conditions have occurred recently on the

southeastern Bering Sea shelf. In addition, an extreme change of physical forcing occurred during 1997 and 1998. Sambrotto *et al.* (1986) measured “new” production after the 1977 regime shift during the PROBES project. A number of biological indices indicate large decreases in productivity associated with the 1989 regime shifts, but a few indices suggest change to higher values (Hare and Mantua, in press). However, there were no direct measurements of total and “new” production after the 1989 regime shift on the southeastern Bering Sea shelf. There is an indication of a decline in carrying capacity of the Bering Sea from a ^{13}C isotope study of bowhead whale baleen (Schell, 2000).

In this study, total, “new”, and “regenerated” production were measured using ^{13}C and ^{15}N tracer techniques during the 1997 and 1998 extreme conditions. It is too early to determine whether or not a regime shift occurred during 1998. Hare and Mantua (in press), however, have suggested that the unusually warm coastal ocean sea surface temperature (SST) era of post-1977 may have ended, as evidenced by the summer temperature difference from 1977-1996 compared with those from 1998-1999. Therefore, the production measurements obtained during the SEBSCC study provide insights into the changes in total, “new”, and “regenerated” production that have taken place during the recent unusual atmospheric-sea ice-ocean conditions. They also indicate how the recent abnormal conditions affected primary production and fate of the resultant organic matter. We were unable to document annual total and “new” production over the southeastern Bering Sea shelf from direct productivity measurements, due to the mismatch of the timing of field observations with actual phytoplankton blooms. However, during 1997, we observed deep nitrate uptake below the pycnocline, which partially explains the observed deep nitrate depletion during the

1997 summer over the middle shelf. We also made several ^{13}C and ^{15}N uptake rate measurements in the abnormal coccolithophorid bloom, to better understand their competition with diatoms for nutrient resources on the southeastern Bering Sea shelf.

2. MATERIALS AND METHODS

Samples were collected during the 1997 and 1998 field seasons of the SEBSCC (Southeastern Bering Sea Carrying Capacity) and IF (Inner Front) studies (May, 1997, June, 1997, September 1997, April 1998, May 1998, and August 1998) (Fig. 3). Water was taken at six depths, which corresponded to the 100, 50, 30, 12, 5, and 1% penetration of the surface photosynthetically active radiation (PAR), using a CTD rosette sampler with 5 or 10 L Niskin bottles at the first early morning station or at a mid-day station. In situ light depths were determined at each productivity station using an underwater PAR sensor on the CTD frame or a secchi disk if an underwater PAR sensor was not available. Water samples from each depth were transferred from the Niskin bottles to a 10 L polycarbonate carboy through a 333 μm mesh net to remove large zooplankton, split into three subsamples, and transferred to 1.2 L polycarbonate incubation bottles. The incubation bottles were covered with neutral density nickel or stainless steel screens to simulate in situ light levels (i.e., 100, 50, 30, 12, 5, and 1%). Each light depth sample was spiked with ^{13}C and ^{15}N and then incubated for 4–6 hours in a deck incubator cooled by running surface seawater. In the first incubation bottle set, between 0.2 and 1 ml of 2 mmol/ml K^{15}NO_3 was added, depending on the nitrate concentration that was expected in the water (added nitrate was ca. 10% of nitrate concentration). In the second and third bottles set, 1 ml of 0.2 mmol/ml $^{15}\text{NH}_4\text{Cl}$ and ^{15}N -urea were inoculated. Each incubation bottle was also inoculated with 1 ml of 2 mg/ml $\text{NaH}^{13}\text{CO}_3$. The incubations were terminated by filtering the water through precombusted GF/F glass fiber filters. The filters were kept frozen until prepared for mass spectrometric analysis at the stable isotope laboratory of the University of Alaska

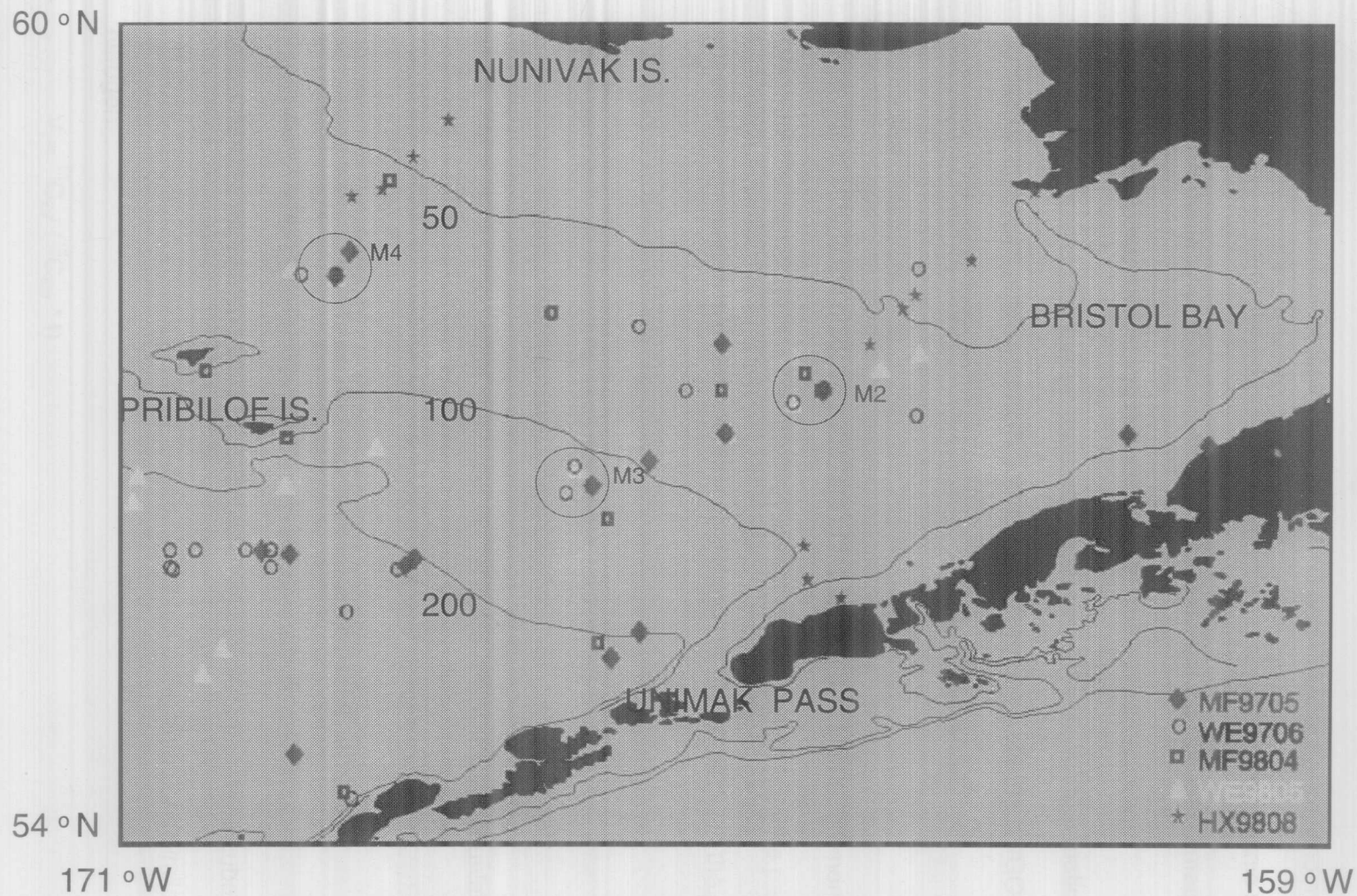


Fig. 3 Station locations of carbon and nitrogen uptake studies over the southeastern Bering Sea shelf. Circles are major mooring locations. The location of the inner, middle, and outer fronts are approximated by the 50, 100, and 200 m isobaths, respectively.

Fairbanks (UAF). In the laboratory, the filters were dried for 24hr at 60°C and then placed in a tin capsule. Isotopic analysis for ^{13}C and ^{15}N abundance, and measurements of the quantity of particulate organic carbon (POC) and particulate organic nitrogen (PON), were performed with a CN analyzer coupled to a Europa 20-20 mass spectrometer.

^{13}C and ^{15}N uptake rates were calculated using the following equations:

(1) Specific nitrogen uptake rates (h^{-1}) were calculated using standard JGOFS procedures (JGOFS, 1990).

$$V_n = {}^{15}\text{N}_{\text{xs}} / ({}^{15}\text{N}_{\text{enr}} * t)$$

where the n in V_n is the nitrogen substrate of incubation (i.e. nitrate, ammonium, and urea) and ${}^{15}\text{N}_{\text{xs}}$ is the excess ^{15}N [the concentration of ^{15}N (atom %) in the particulate phase after incubation minus the natural abundance of ^{15}N (atom %) in the particulate phase (0.366%)]. t is incubation time (hrs).

(2) ${}^{15}\text{N}_{\text{enr}}$ is the ^{15}N enrichment in the dissolved fraction.

$${}^{15}\text{N}_{\text{enr}} = [100 * ({}^{15}\text{N} / ({}^{15}\text{N} + {}^{14}\text{N})) - {}^{15}\text{N}_n]$$

where ${}^{15}\text{N}$ is the concentration of labeled N, ${}^{14}\text{N}$ is the concentration of unlabelled N, and ${}^{15}\text{N}_n$ is the natural abundance of ^{15}N .

(3) Absolute uptake rates (ρ , transport rates) were calculated as

$$\rho_n = \text{PON}_i * V_n$$

where PON_i is the concentration of particulate organic nitrogen after incubation.

(4) Specific carbon uptake rates (h^{-1}) were calculated using equations similar to those for nitrogen.

$$V_c = {}^{13}\text{C}_{\text{xs}} / ({}^{13}\text{C}_{\text{enr}} * t)$$

where $^{13}\text{C}_{\text{xs}}$ is the excess ^{13}C [the concentration of ^{13}C (atom %) in the particulate phase after incubation minus the natural abundance of ^{13}C (atom %) in the particulate phase (1.108%)].

(5) $^{13}\text{C}_{\text{enr}}$ is the ^{13}C enrichment in the dissolved fraction.

$$^{13}\text{C}_{\text{enr}} = [100 * (^{13}\text{C} / (^{13}\text{C} + ^{12}\text{C})) - ^{13}\text{C}_n]$$

Where ^{13}C is the concentration of labeled C, ^{12}C is the concentration of unlabelled C, and $^{13}\text{C}_n$ is the natural abundance of ^{13}C .

(6) Absolute uptake rates (ρ , transport rates) were calculated as

$$\rho_c = \text{POC}_f * V_c$$

Where POC_f is the concentration of particulate organic carbon after incubation.

Daily values of productivity were estimated by multiplying hourly values by the hours of daylight (from 30 minutes after sunrise to 30 minutes before sunset). Water column uptake rates were integrated from surface to 1% light depths to obtain areal values. Nutrient (nitrate, silicate, phosphate, ammonium, and nitrate) concentrations were measured by T. E. Whitledge on shipboard using an automated nutrient analyzer (ALPKEM) following Whitledge *et al.* (1981). After inorganic nutrient analysis, samples for urea and DON analysis were frozen and analyzed in the shoreside laboratory. Chlorophyll samples were collected at each light depth and kept frozen until analysis in the laboratory by D. Stockwell, following Parsons *et al.* (1984).

3. RESULTS

3.1 Hydrography

3.1.1 1997 across Bering Sea shelf hydrographic properties

Hydrographic data obtained in May 1997 indicated an earlier than normal spring stratification. The outer shelf had homogeneous surface and near bottom layers separated by a stratified zone, there was a strongly two-layered middle shelf domain, and the water column was vertically well mixed at the coastal end of the across shelf transect (Fig. 4). The middle front zone was evident between station 27 and 32 in the sigma-t depth profiles. A cold water mass, produced by melting sea ice, was evident throughout the middle shelf domain. We can easily identify this water mass by its conspicuous cold temperature (ranging from -1°C to 2°C) and low salinity (< 31.4 psu). Salinity was a major factor controlling the density of this water mass. A high fluorescence signal was observed in the outer shelf domain and the middle front. Chlorophyll (as evidenced by fluorescence) had already settled to the bottom in the middle shelf area. The across shelf transport of slope water was evident in the high temperature and salinity signals of the bottom layer of the outer shelf, $>4^{\circ}\text{C}$ and > 32.7 psu (Fig.4).

During the June 1997 cruise, strong stratification occurred over the entire cross shelf section and temperatures of the cold water mass were increased by ca. 1°C (Fig. 5). An upward dome in the structure of the sigma-t profile was observed between station 66 and 67. The salinity profile suggests an ascent of deep water (> 32.0 psu) at this station. Generally, in June 1997 chlorophyll concentrations were low over the entire

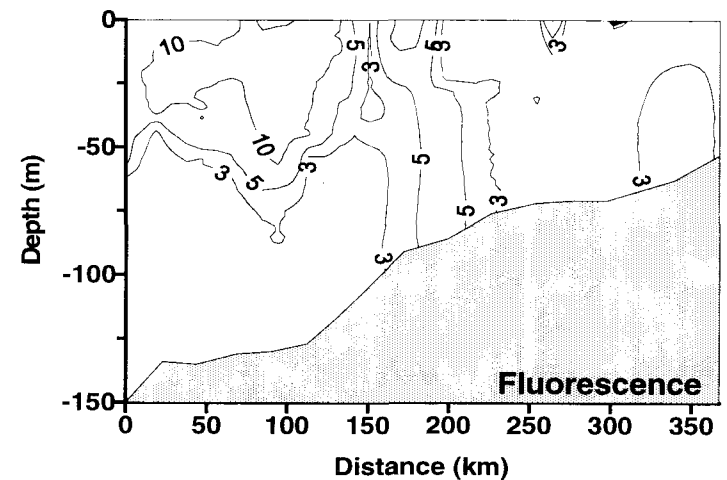
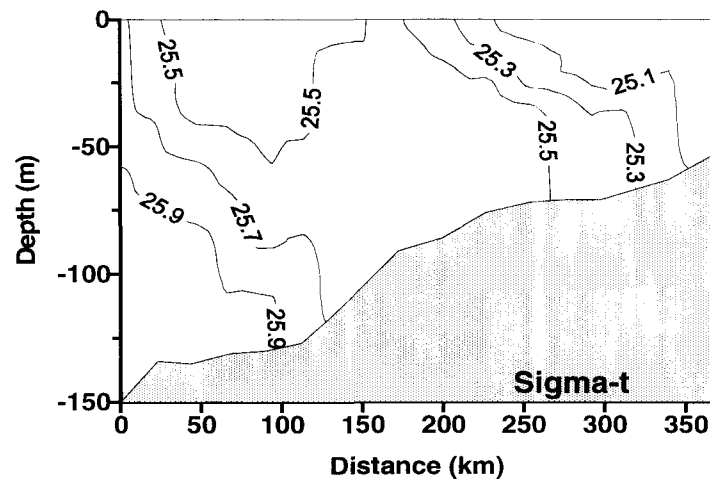
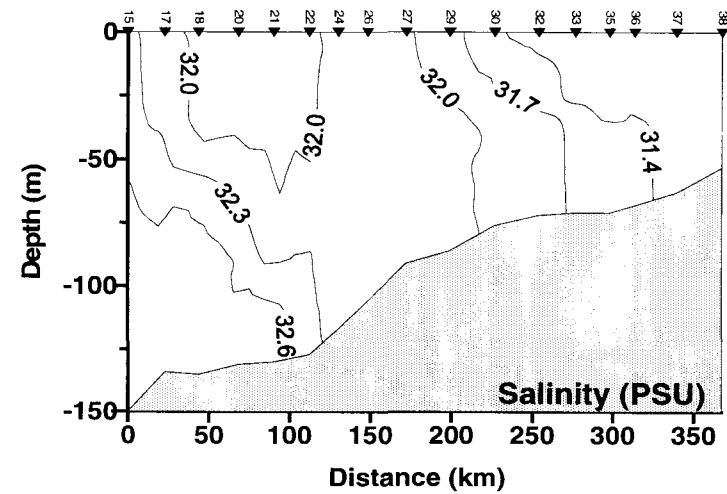
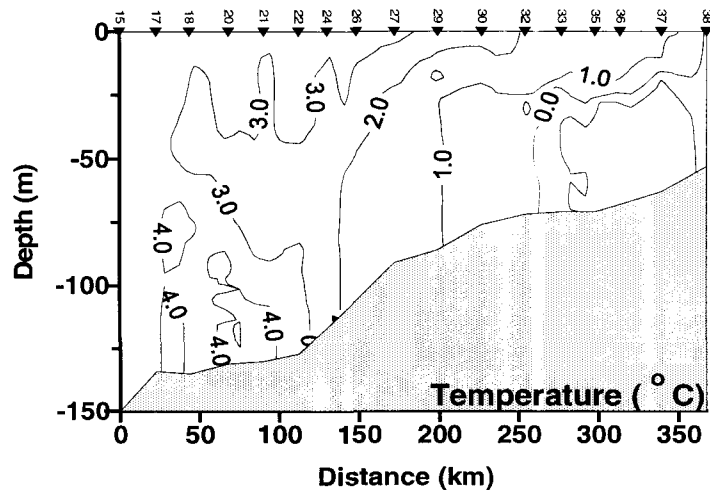


Fig. 4 Distributions of temperature, salinity, sigma-t, and fluorescence for an across Bering Sea shelf transect during 5 - 7 May 1997. Across shelf CTD station numbers are listed at the top of figures.

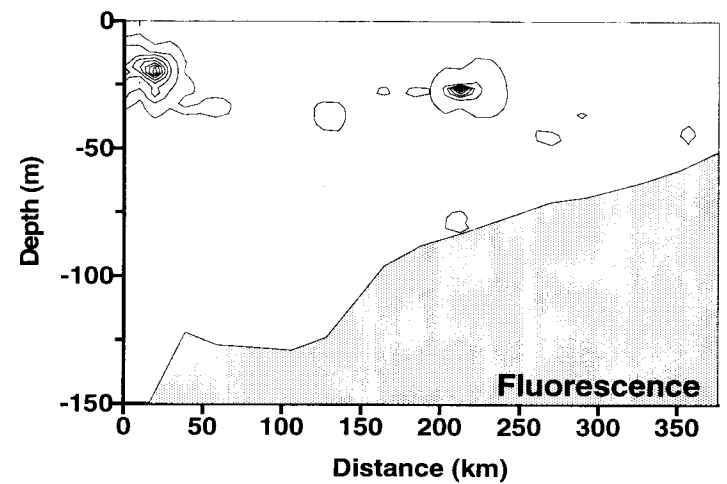
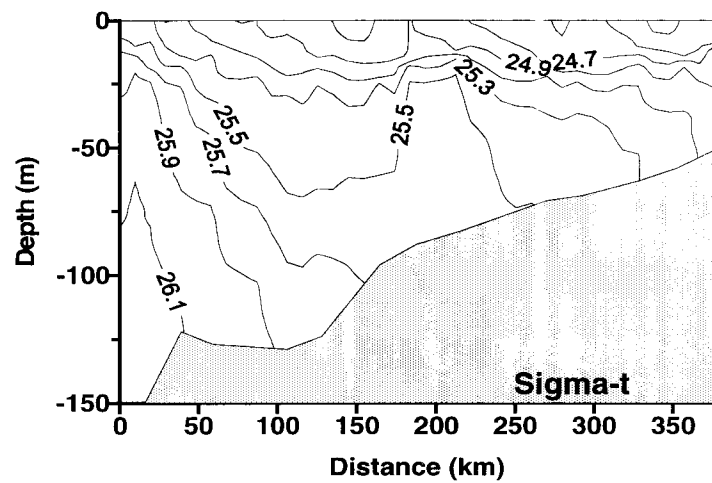
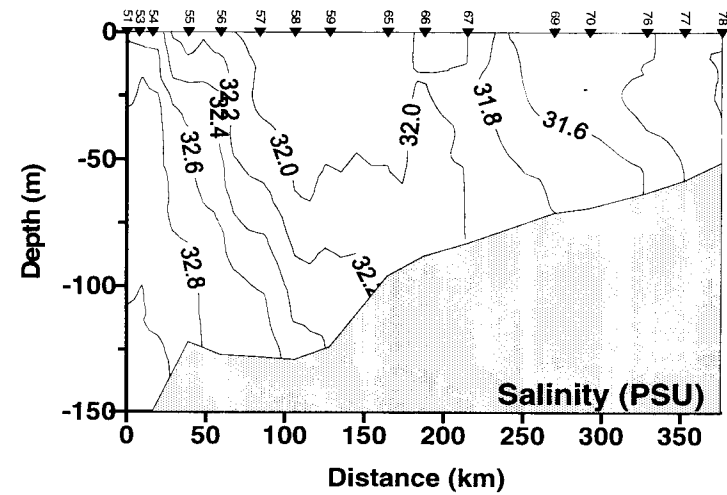
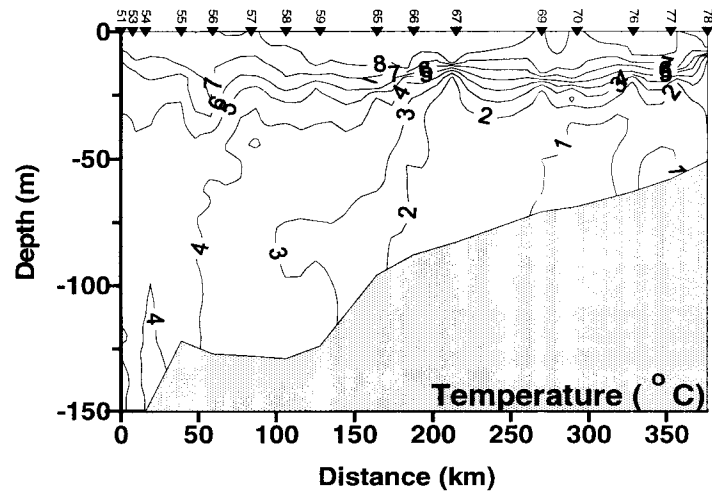


Fig. 5 Distributions of temperature, salinity, sigma-t, and fluorescence for an across Bering Sea shelf transect during 17 - 19 June 1997. Across shelf CTD station numbers are listed at the top of figures.

shelf area. A relatively high chlorophyll concentration layer was observed at 30m depth around the 80m isobath, which corresponded to the upward dome structure of sigma-t at stations 53 and 66.

3.1.2 1997 along shelf hydrographic properties

During the May 1997 SEBSCC cruise, the water column along the 70m isobath showed complete vertical mixing at the northern end with some areas of slight stratification in the south (Fig. 6). Generally, the temperature of this section was very low and was below 0 °C in most of the water column. Salinity and density were nearly homogeneous with depth and decreased northward, presumably due to the retreating sea ice. Salinity probably controlled the distribution of density. Fluorescence showed strong patchiness around station 45 located north of mooring 2 (M2) where more stratification developed (Fig. 6).

During the June 1997 cruise, temperature and sigma-t profiles showed strong stratification over the entire along shelf section (Fig. 7). Temperature was an important factor controlling the distribution of density. Salinity isopleths were vertical and did not show a systematic decrease toward the north. Salinity of the northern water mass increased by about 0.2 psu compared to that during the May cruise, probably due to the advection of high salinity water from the slope water mass. There was slightly higher salinity water (> 31.5 psu) at the bottom of station 84. Fluorescence was low throughout the section (Fig. 7). During both May and June 1997, the 70 m isobath transect contained the cold pool water (< 2 °C) that was formed over the shelf during winter.

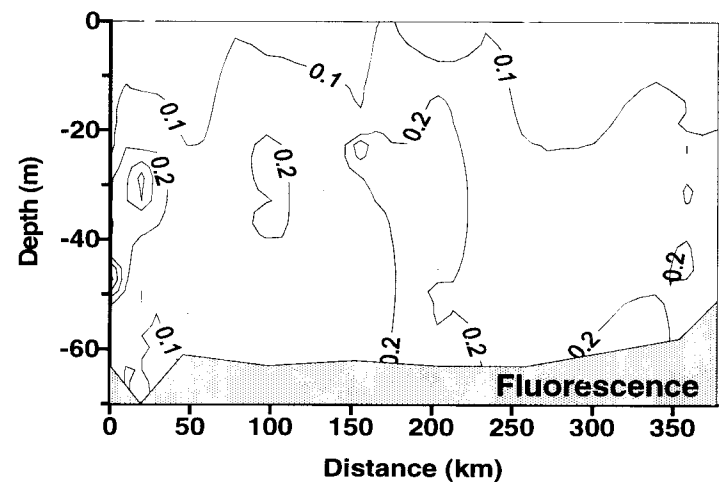
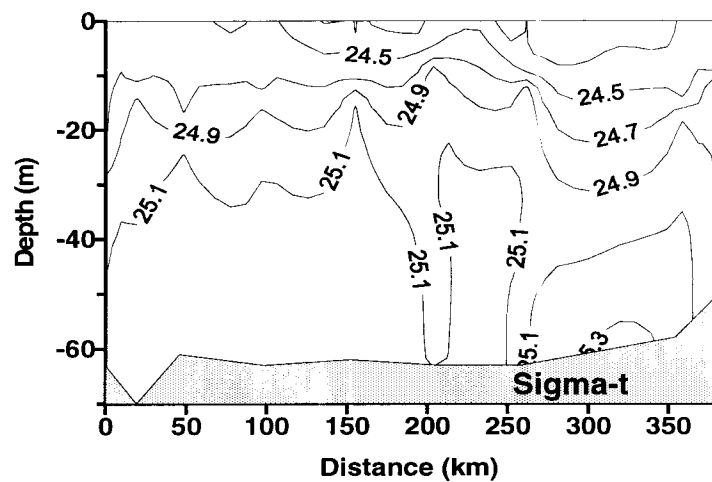
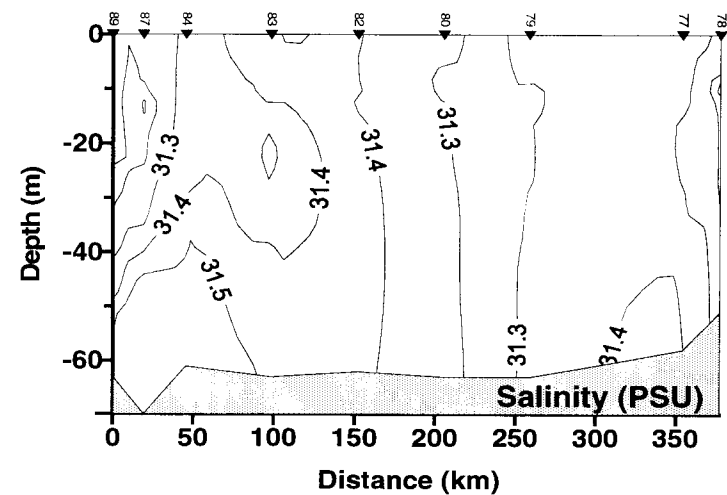
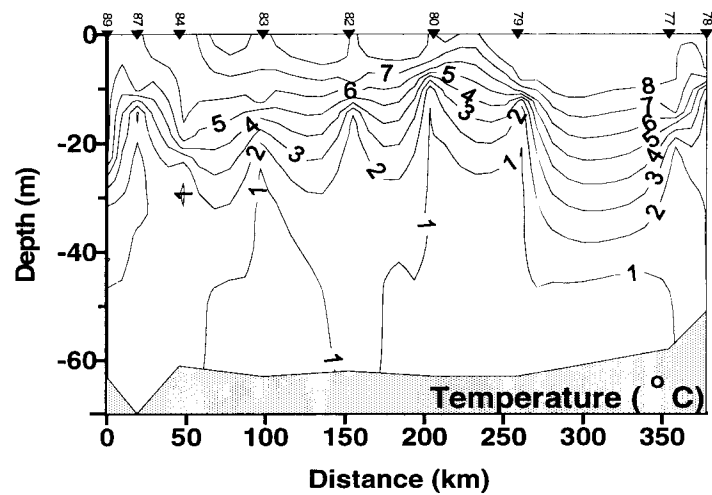


Fig. 7 Distributions of temperature, salinity, sigma-t, and fluorescence along the Bering Sea shelf 70m isobath during 19 - 20 June 1997. Along shelf CTD station numbers are listed at the top of figures.

3.1.3 1998 across Bering Sea shelf hydrographic properties

During April 1998, the water column over the entire across shelf section (Fig. 8) was completely mixed due to frequent storm wind-mixing events. The temperature of the coldest water of the section was 1.2 °C in April 1998 and was higher than in May and June of 1997. Salinity was greater than 31.8 psu over the entire shelf area, and was at least 0.4 psu higher than in May 1997, probably due to an increase in the advection of slope water (Stabeno *et al.*, 2000). The density distribution was determined by both salinity and temperature. The areal coverage of the cold pool ($< 2^{\circ}\text{C}$) was much less than in May and June of 1997. Fluorescence over the entire shelf was low except for the surface water over mooring 2 (M2) (located at station 7). Also, there was across shelf transport of slope water below 100m over the outer shelf. Temperature and salinity were $>4^{\circ}\text{C}$ and > 32.6 psu, respectively.

During May 1998, the water column structure was generally similar to that encountered in April 1998 except for an increase in temperature (ca. 1.0 °C). The water was also vertically well mixed to 90m (Fig. 9). A low fluorescence signal was evident over most of water column except for the inner end of the cross shelf transect where relatively high fluorescence extended throughout the water column near mooring 2 (M2).

3.1.4 1998 along shelf hydrographic properties

During April 1998, temperature and salinity along the 70m isobath were vertically homogeneous and also showed the influence of the retreating sea ice (a decrease of salinity and density toward the north) (Fig. 10). An onshore transport of slope water is evident over the shelf area (higher temperature and salinity water, $> 2.6^{\circ}\text{C}$, > 32.26 psu,

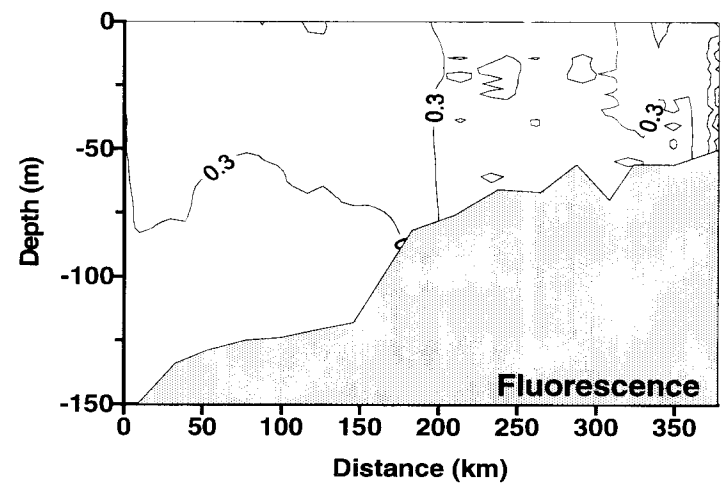
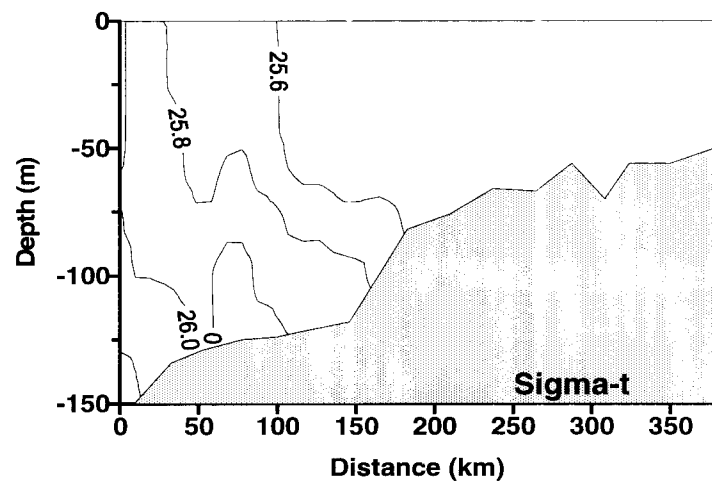
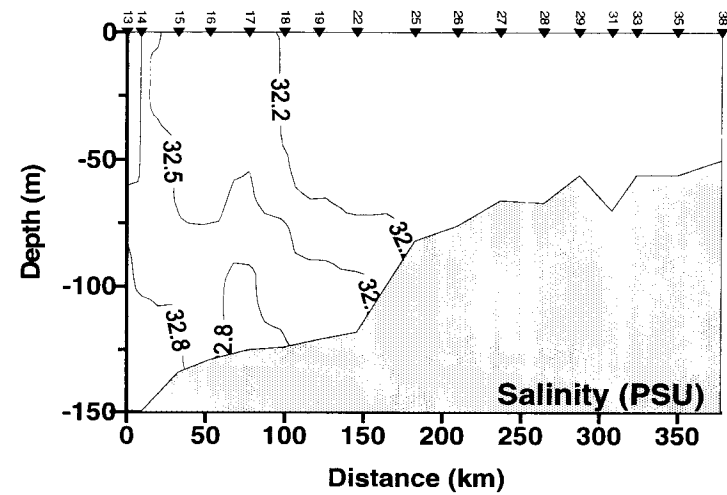
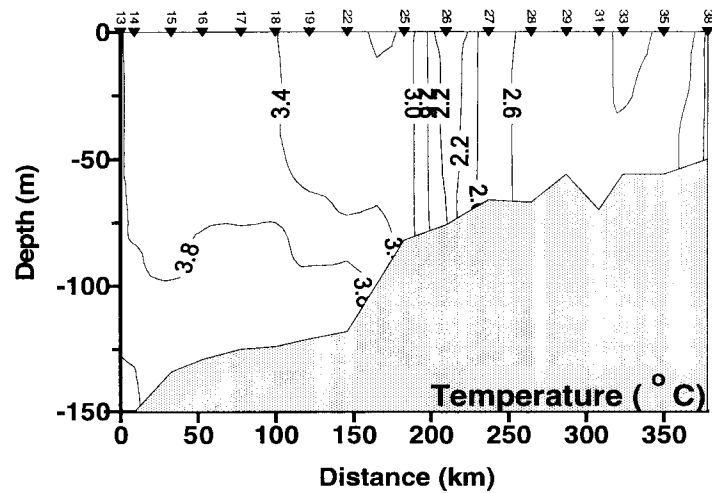


Fig. 9 Distributions of temperature, salinity, sigma-t, and fluorescence for an across Bering Sea shelf transect during 10 - 12 May 1998. Across shelf CTD station numbers are listed at the top of figures.

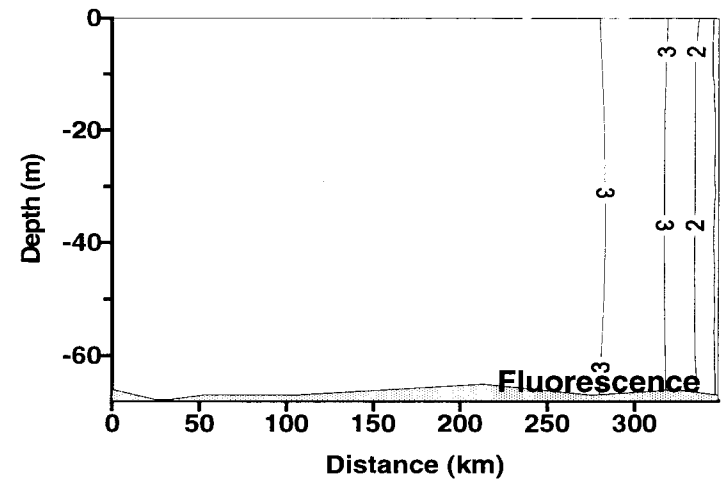
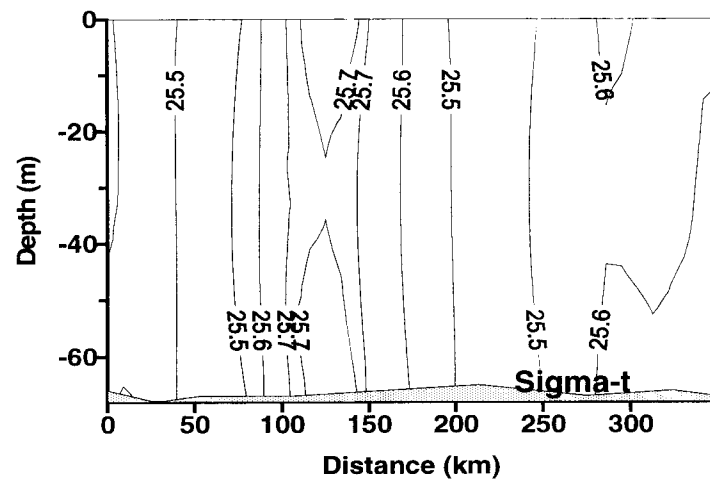
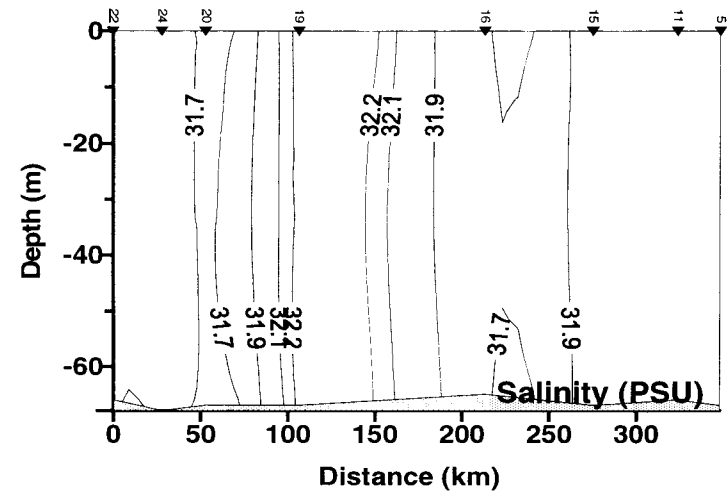
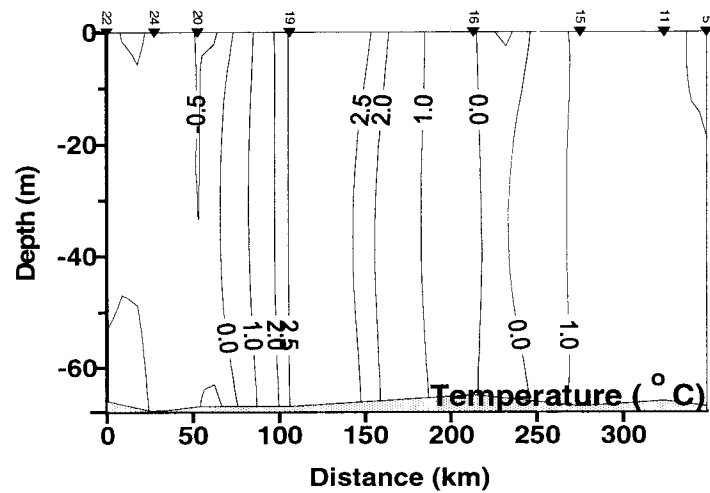


Fig. 10 Distributions of temperature, salinity, sigma-t, and fluorescence along the Bering Sea shelf 70m isobath during 16 - 18 April 1998. Along shelf CTD station numbers are listed at the top of figures.

respectively) between stations 19 and 16 (17 April 1998) (Fig. 10). During May 1998, the water column structure was similar to that encountered in April 1998. An onshore intrusion of slope water occurred over the shelf area between stations 42 and 41 (13 May 1998) (Fig. 11). Both salinity and temperature were important in determining the distribution of density along the 70m isobath transect during both April and May 1998.

3.2 Nutrients

3.2.1 1997 across shelf nutrient distributions

During May 1997, nitrate was depleted in the upper 40-50 m of the water column over most of the shelf (Fig. 12). There were high nitrate concentrations ($> 20 \mu\text{M}$) at 130m over the outer shelf, probably due to the transport of slope water and also to relatively high nitrate concentrations (ca. $10 \mu\text{M}$) in the cold pool. Surface nitrate concentrations were relatively high ($> 5 \mu\text{M}$) near the middle frontal zone. Ammonium concentrations were less than $4 \mu\text{M}$ over most of the shelf area but showed high concentrations ($4 - 14 \mu\text{M}$) in the entire water column around mooring 2 (M2) (station 36). Distributions of silicate and phosphate were similar to those of nitrate. During June 1997, nitrate and silicate were depleted over most of the water column in the middle shelf domain, but showed high concentrations at the bottom of the outer shelf (Fig. 13). Nitrate concentrations were less than $5 \mu\text{M}$ over the entire middle shelf water column and the upper 50m of the outer shelf (Fig 12). Across shelf transport of high nutrient water was evident in the nitrate, silicate, and phosphate profiles. Silicate distributions resembled those of nitrate, but concentrations remained greater than $5 \mu\text{M}$ over the

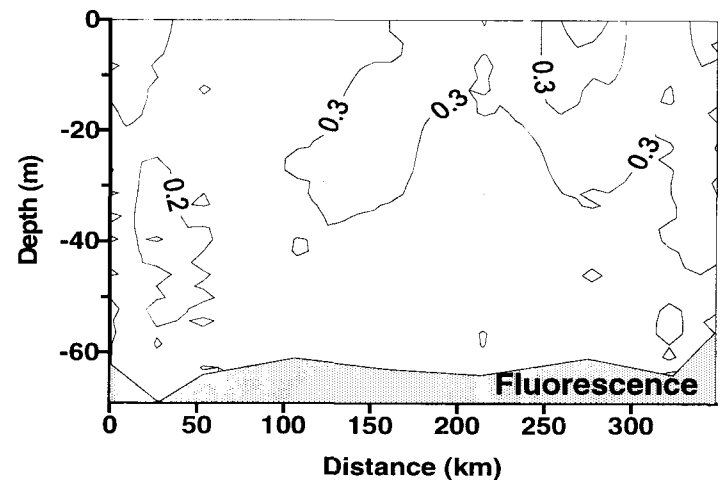
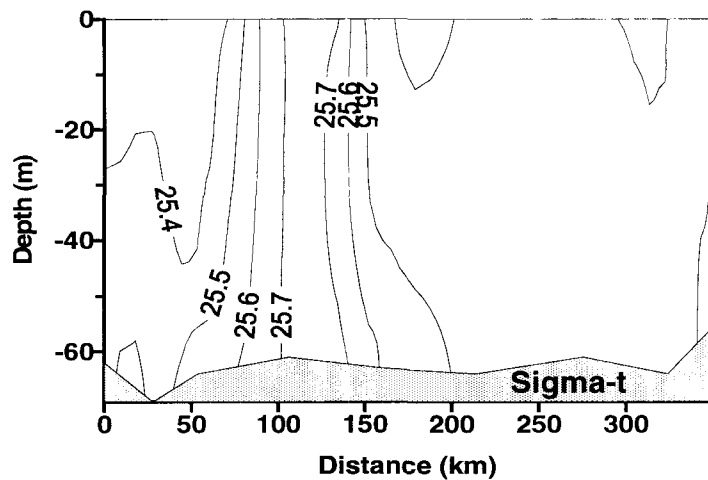
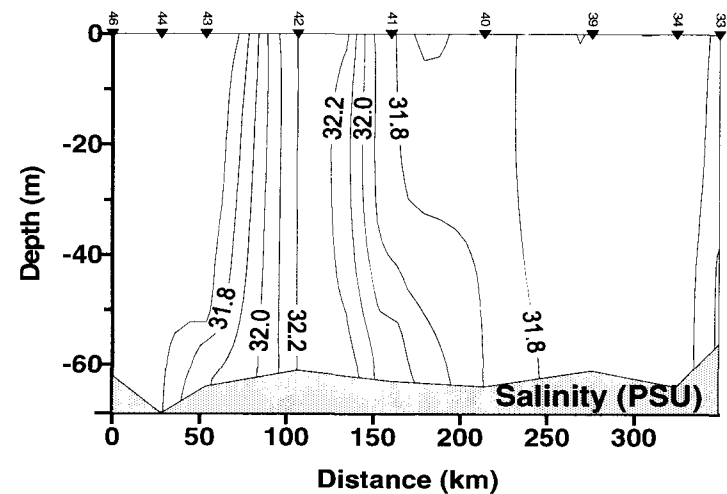
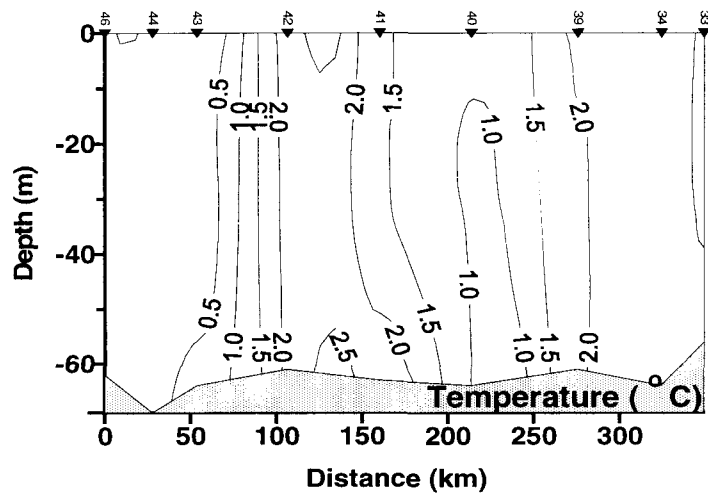


Fig. 11 Distributions of temperature, salinity, sigma-t, and fluorescence along the Bering Sea shelf 70m isobath during 12 - 13 May 1998. Along shelf CTD station numbers are listed at the top of figures.

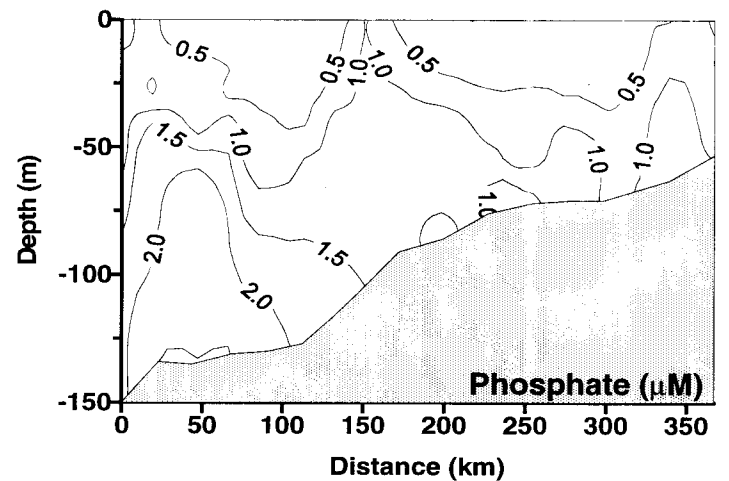
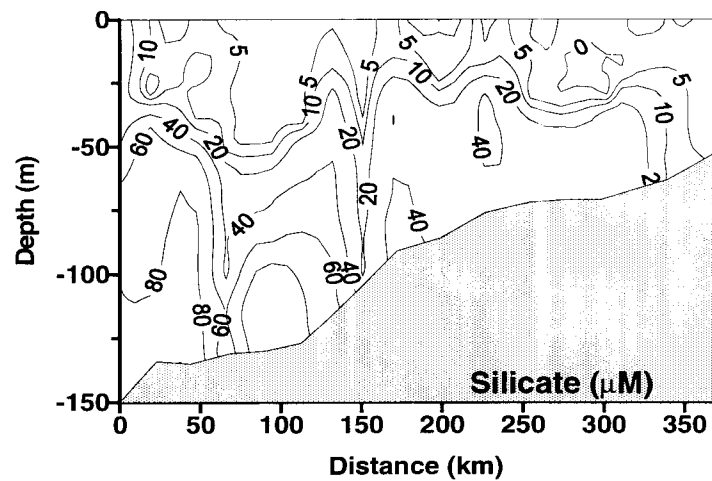
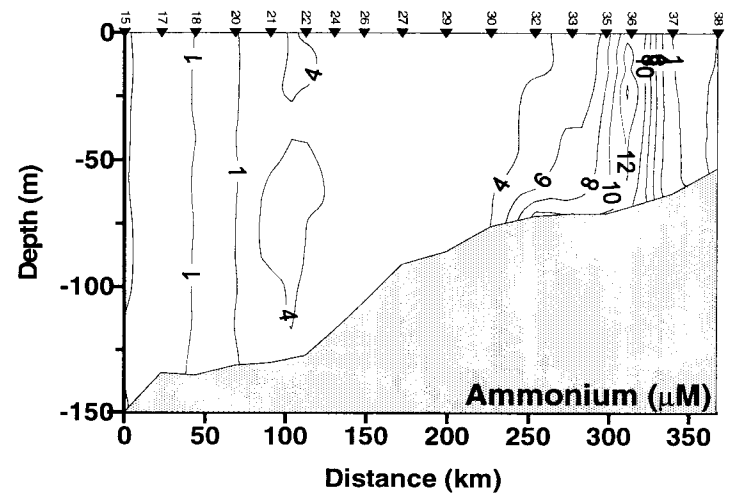
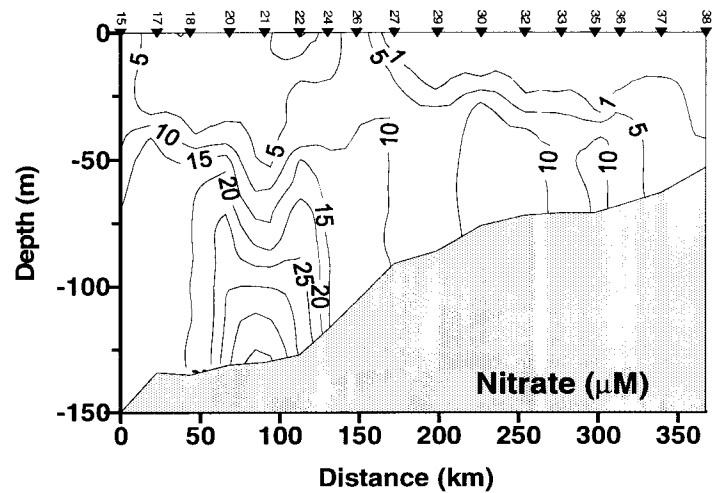


Fig. 12 Distributions of nitrate, ammonium, silicate, and phosphate for an across Bering Sea shelf transect during 5 - 7 May 1997. Across shelf CTD station numbers are listed at the top of figures.

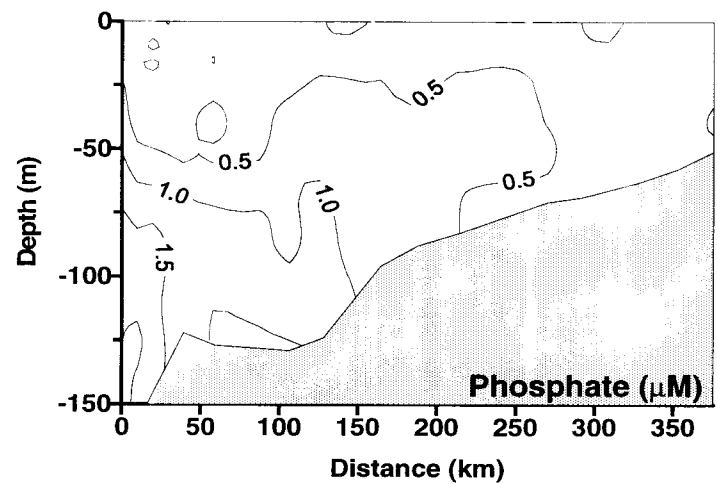
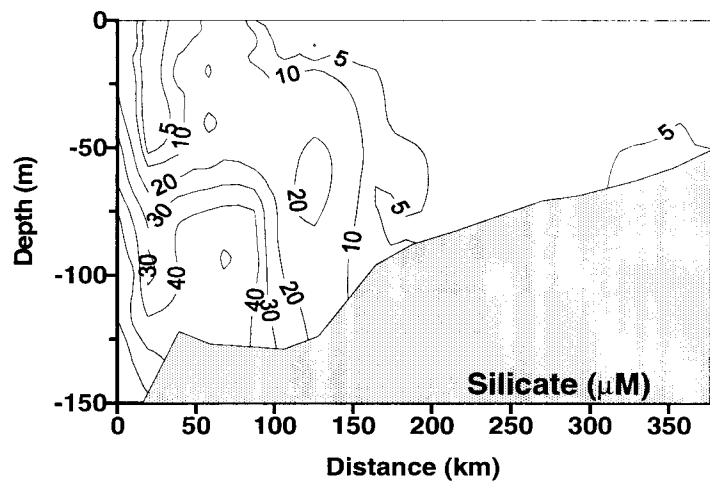
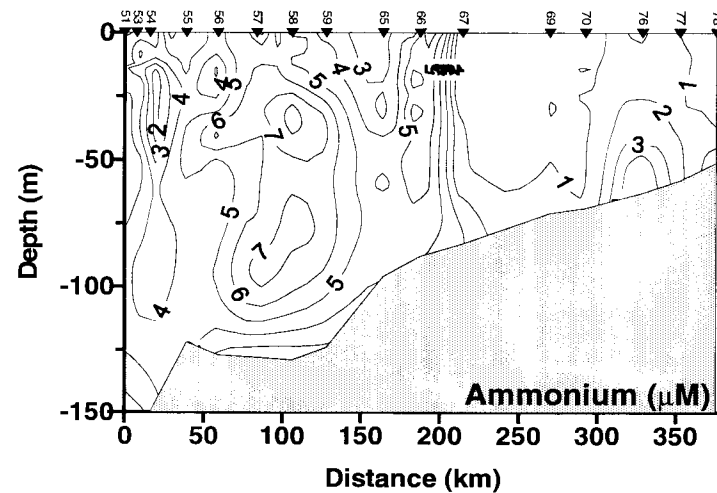
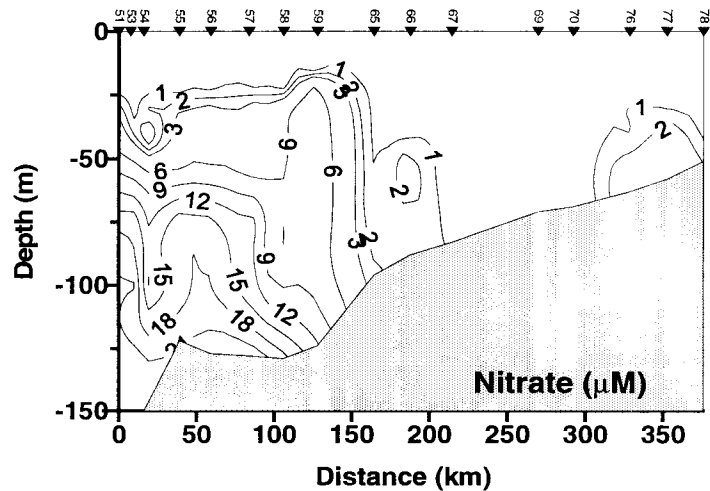


Fig. 13 Distributions of nitrate, ammonium, silicate, and phosphate for an across Bering Sea shelf transect during 17 - 19 June 1997. Across shelf CTD station numbers are listed at the top of figures.

outer shelf. Ammonium concentrations were relatively high (3-9 μM) over the outer shelf region.

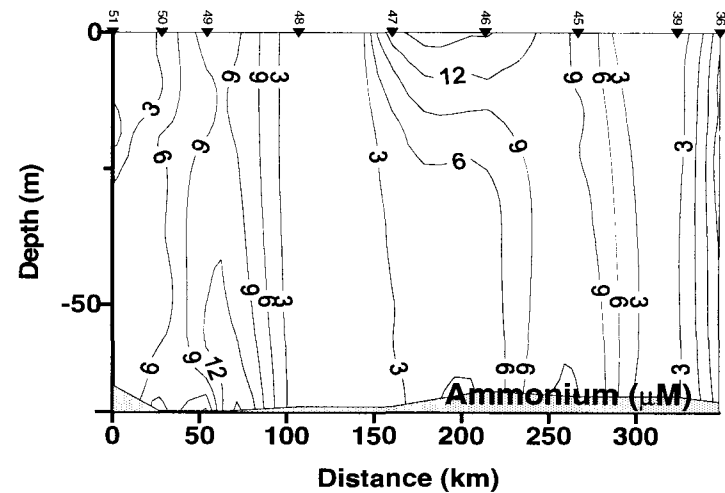
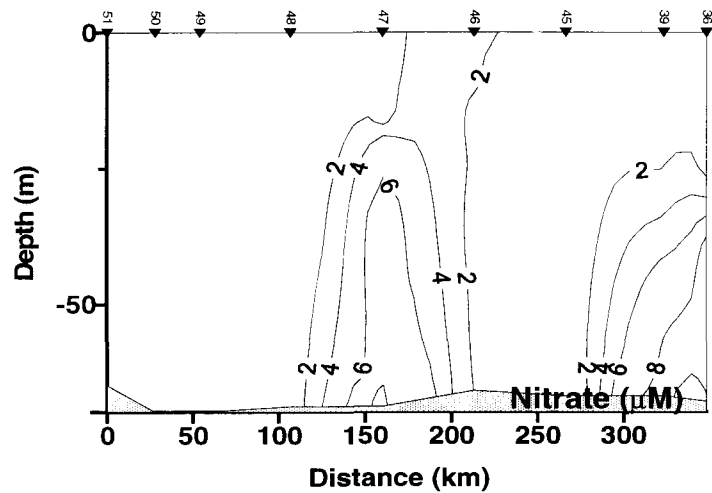
There are two plausible explanations for the high ammonium concentrations observed over the outer shelf during 1997. First, ammonium was released during zooplankton grazing. Sambrotto (1983) measured ammonium excretion by macrozooplankton. Ammonium concentrations increased in the containers with larger numbers of macrozooplankton, while showing no increase in containers with small numbers of macrozooplankton and the control. Second, ammonium was supplied from the middle shelf to the outer shelf in the fine structure water ubiquitous in this region (Whitledge *et al.*, 1986).

3.2.2 1997 along Bering Sea shelf nutrient distributions

During May 1997, nitrate was depleted over most of the water column except for the deep water column in the middle of the along shelf transect and around mooring 2(M2) (Fig. 14). Silicate and phosphate distributions were similar to those of nitrate. Ammonium concentrations were high throughout most of the water column, but had relatively low concentrations in the middle of the transect. High nitrate, silicate, and phosphate concentrations around station 47 were possibly related to the advection of nutrient-rich water from the slope area. During June 1997, concentrations of all nutrients (nitrate, ammonium, silicate, and phosphate) were reduced compared to those of May 1997 (Fig. 15).

3.2.3 1998 across shelf nutrient distributions

During April 1998, high nitrate concentrations were observed throughout the water column ($> 12 \mu\text{M}$) over the entire shelf area (Fig. 16). High nitrate and silicate



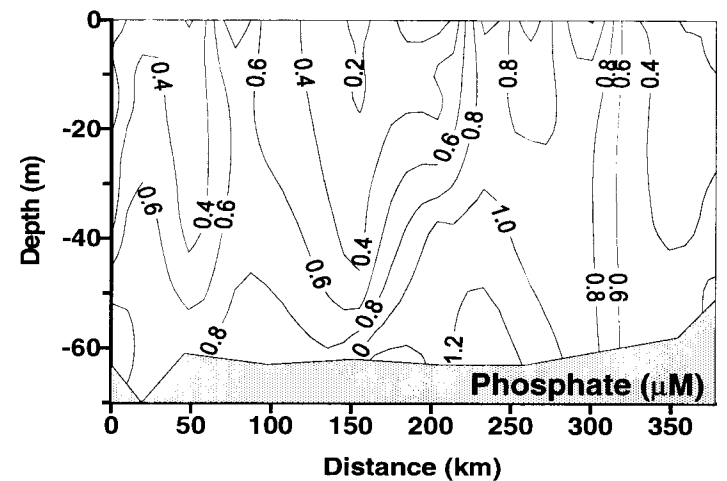
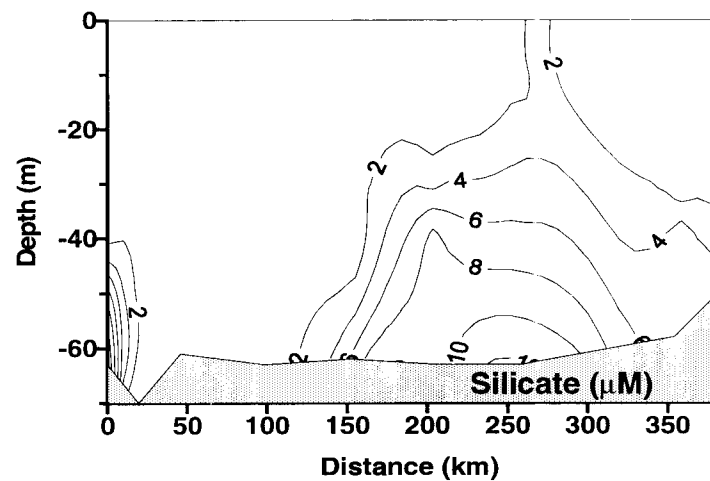
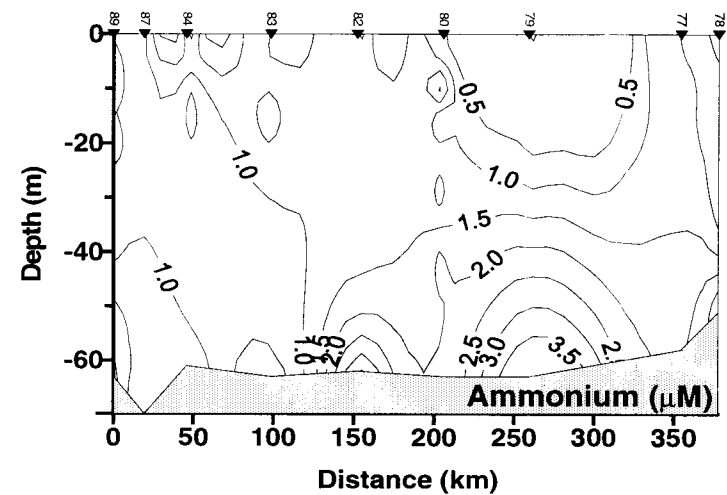
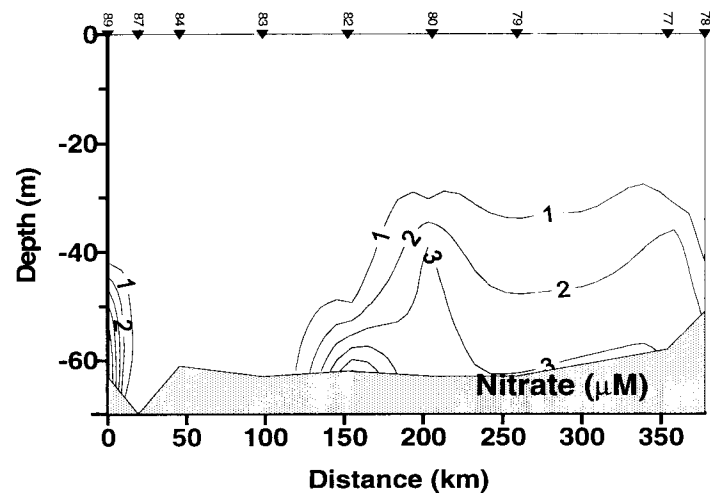


Fig. 15 Distributions of nitrate, ammonium, silicate, and phosphate for along the Bering Sea shelf 70m isobath during 19-20 June 1997. Along shelf CTD station numbers are listed at the top of figures.

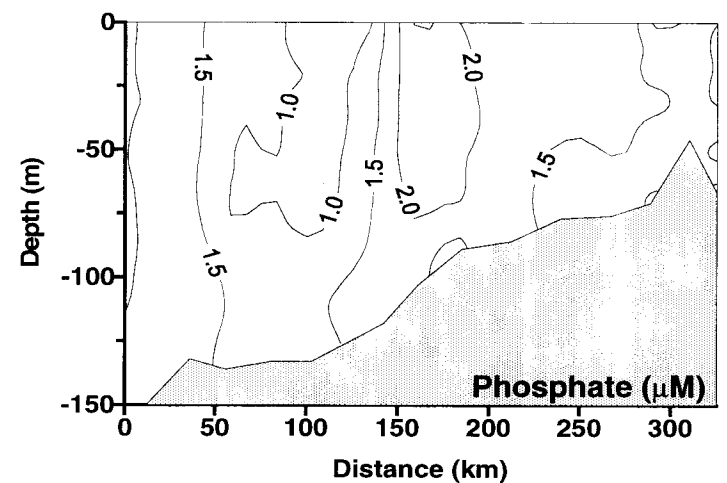
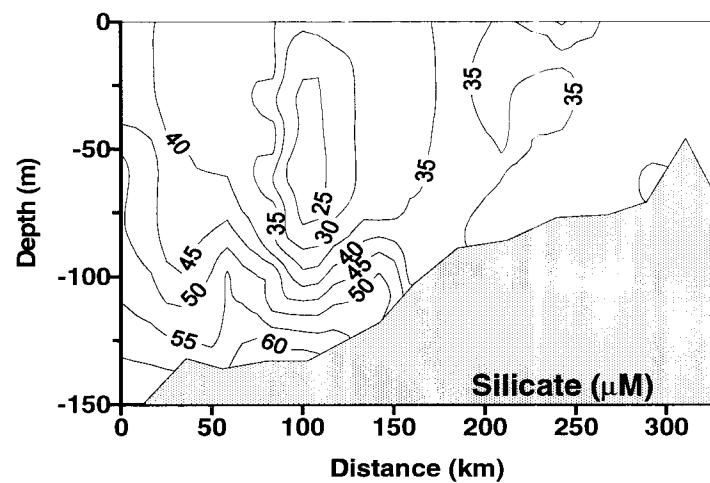
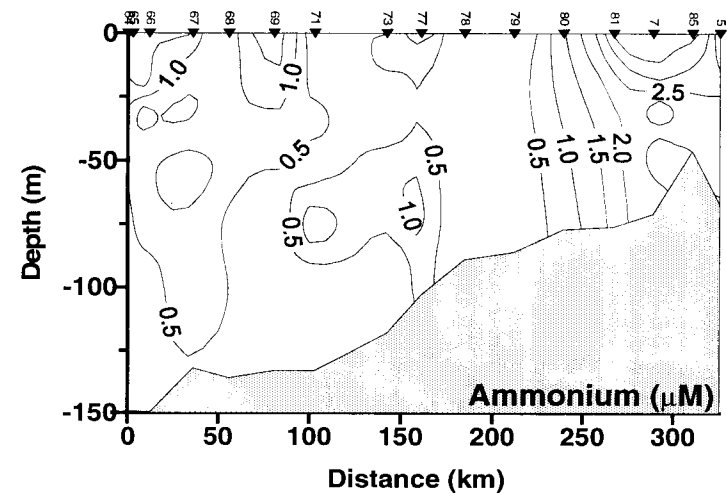
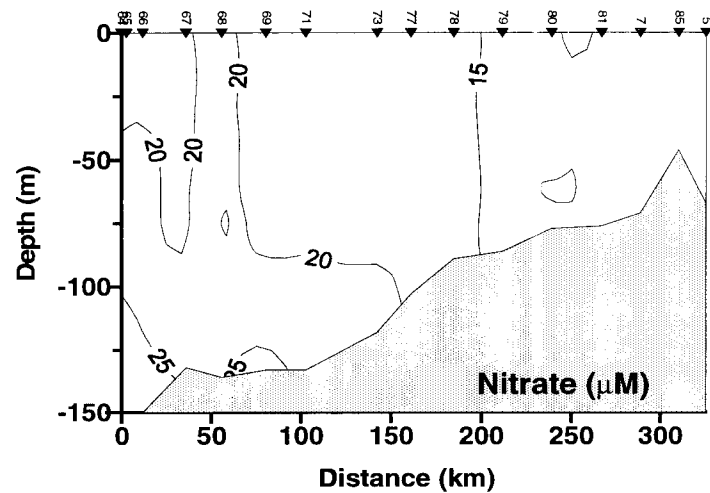


Fig. 16 Distributions of nitrate, ammonium, silicate, and phosphate for an across Bering Sea shelf transect during 24 - 26 April 1998. Across shelf CTD station numbers are listed at the top of figures.

concentrations at the bottom of station 68 implied that the advection of nutrient rich slope water was the source of nutrients to the shelf area. Ammonium concentrations ranged from 0.1 to 3.6 μM over the entire shelf area. Relatively high ammonium concentrations ($> 2.5 \mu\text{M}$) were observed in the surface layer near mooring 2 (M2) (station 7, Fig. 16). During May 1998, nitrate concentrations were still high ($> 8 \mu\text{M}$) in the middle shelf but were decreased by about 5 μM compared to April values. Ammonium concentrations were significantly different from April 1998 and ranged from 4 μM to 24 μM . The highest ammonium concentrations ($> 20 \mu\text{M}$) occurred near the 100 m isobath region (Fig. 17).

There are two plausible explanations for the high 1998 ammonium concentrations observed over the entire shelf. First, the high ammonium concentrations were probably related to zooplankton grazing activity. As mentioned earlier, large numbers of zooplankton can cause an increase in ammonium concentrations through increased grazing activity at elevated temperatures. During May 1998, the heat content of the water column over the entire shelf was high (Stabeno *et al.*, 2000). Therefore, the maturation and growth of zooplankton may have been accelerated over the entire shelf (Smith and Vidal, 1986). Second, the effect of increased temperatures on microbial remineralization may have resulted in the observed high ammonium concentrations. During 1997, average temperatures of the subsurface water column over the middle shelf were cold (Stabeno *et al.*, 2000). This likely resulted in less decomposition of spring bloom organic material settling from the upper euphotic layer to the bottom layer. Any organic material remaining from the 1997 production cycle was also probably available for decomposition by microorganisms with elevated activity because of increased 1998 water temperatures.

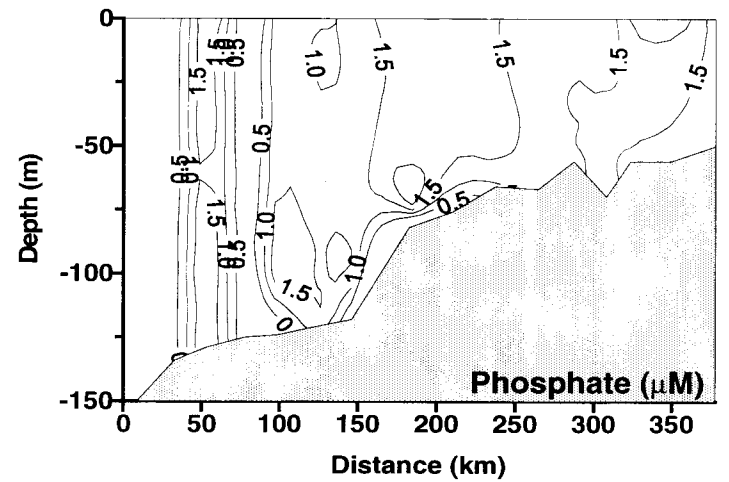
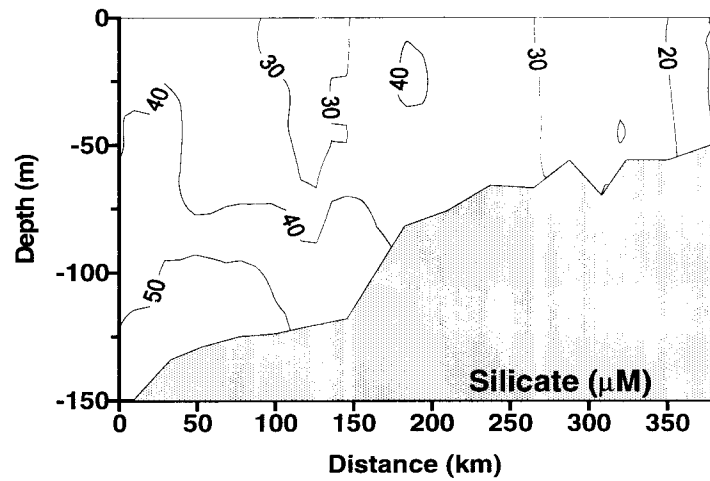
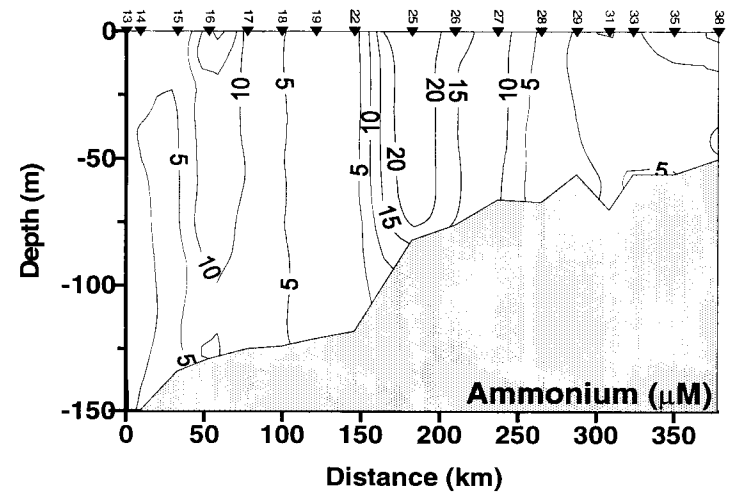
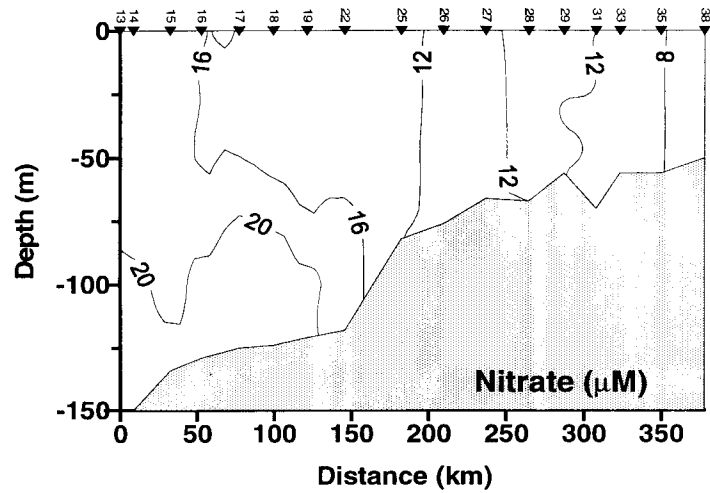


Fig. 17 Distributions of nitrate, ammonium, silicate, and phosphate for an across Bering Sea shelf transect during 10 - 12 May 1998. Across shelf CTD station numbers are listed at the top of figures.

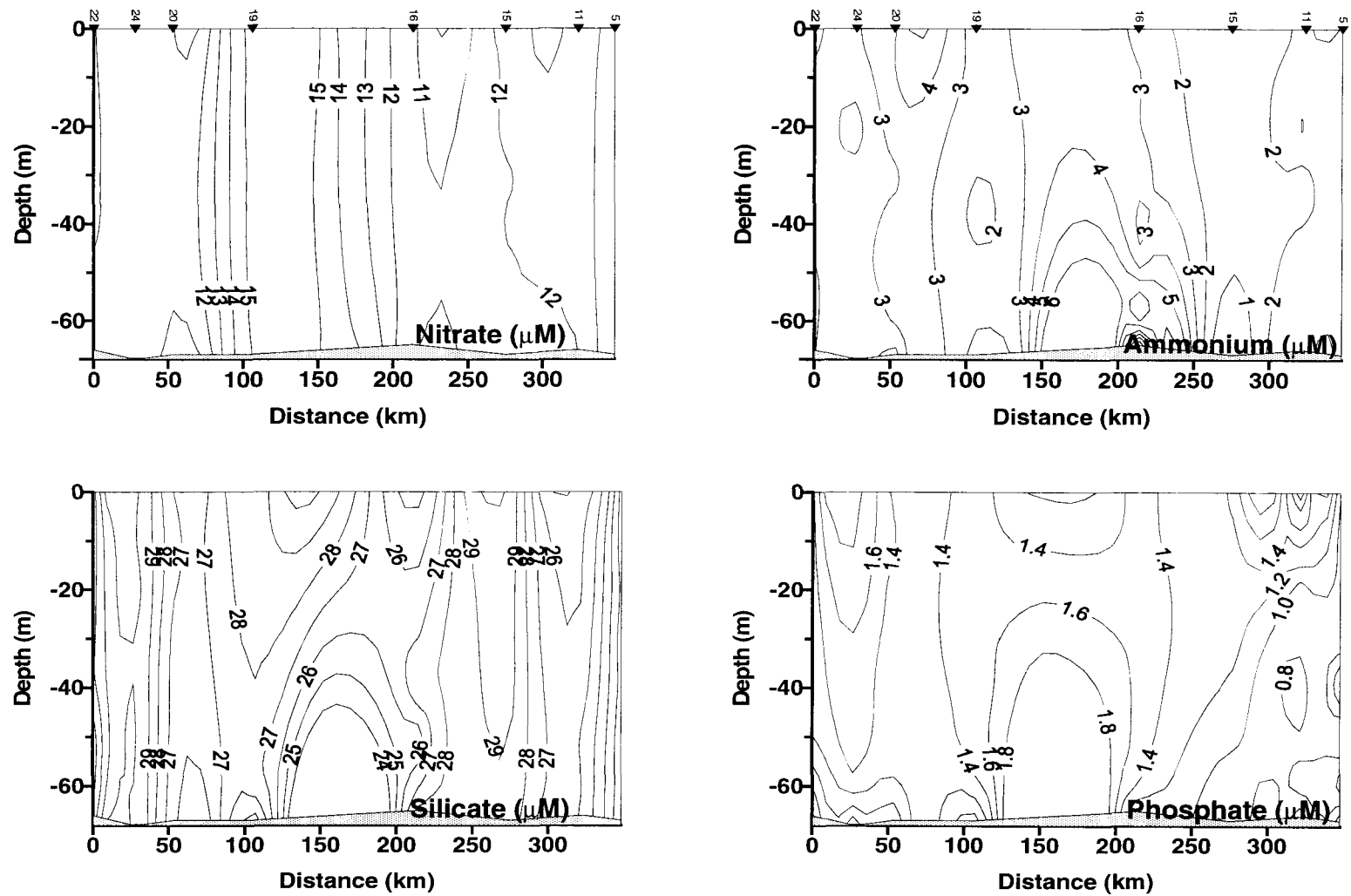
3.2.4 1998 along shelf nutrient distributions

During April 1998, nitrate concentrations were vertically homogeneous and were high around station 19 that contained waters with high temperatures and salinities (Fig. 18). Ammonium concentrations in the middle shelf were less than $4 \mu\text{M}$ over most of the water column except for high concentrations (ca. $6 \mu\text{M}$) at the bottom between stations 19 and 16. Silicate concentrations ranged from 24.7 to $30.9 \mu\text{M}$ over the entire transect and were vertically homogeneous. The distribution of phosphate was similar to that of ammonium and concentrations ranged from 0.66 to $1.86 \mu\text{M}$. High phosphate concentrations coincided with high ammonium concentrations (Fig. 18). During May 1998, the general pattern of nutrient distributions was similar to those of April. Ammonium concentrations were higher over the entire water column ($>4 \mu\text{M}$) of the transect when compared with April 1998, however, other nutrients remained about the same level (Fig. 19).

3.3 Carbon uptake

3.3.1 1997 ^{13}C uptake spatial distributions

In May, ^{13}C uptake values ranged from 85.6 to $1983.3 \text{ mg C m}^{-2} \text{ day}^{-1}$ over the Bering Sea shelf. The average vertically integrated carbon uptake of the middle shelf ($138.8 \text{ mg C m}^{-2} \text{ day}^{-1}$) was lower than that of the outer shelf ($578.4 \text{ mg C m}^{-2} \text{ day}^{-1}$) (Table 2). The highest vertically integrated carbon uptake rate ($1983.3 \text{ mg C m}^{-2} \text{ day}^{-1}$) occurred at the middle front station where high nutrient water ascends to the surface



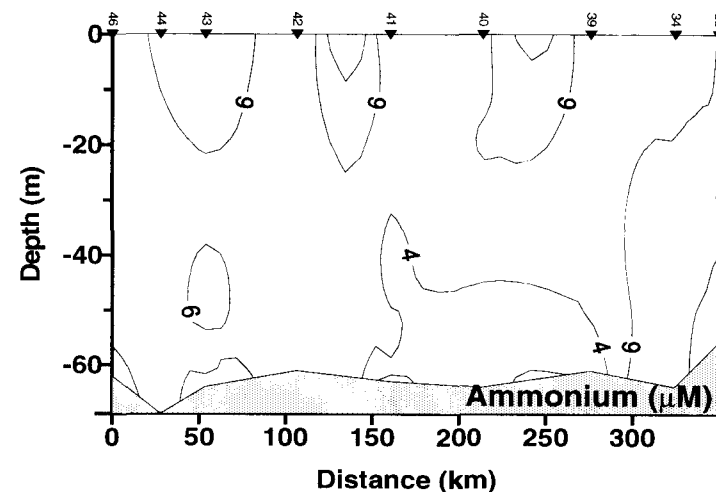
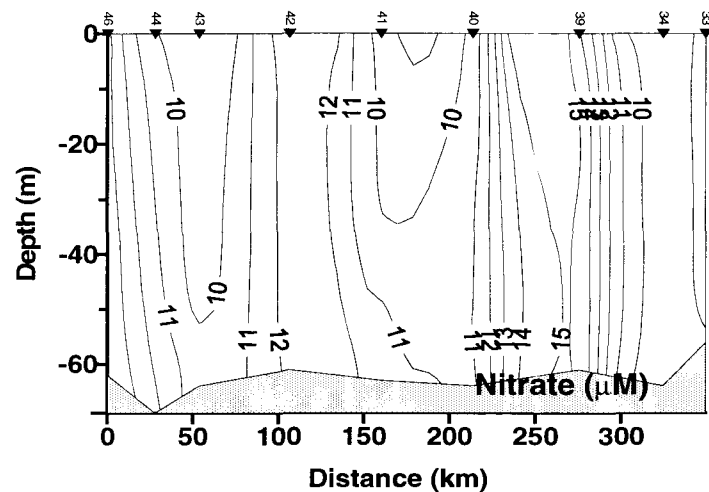


Table 2. Averaged vertically integrated carbon uptake rates over the Bering Sea during 1997 and 1998 (mg C m⁻² day⁻¹).

Year	Date	Inner shelf	Middle shelf	Outer shelf	Shelf break	Open ocean
97	May (4-12)	255.1	138.8	578.4	1271.2	711.3
	June (11-25)	107.9	122.2	292.7	170.7	479.4
98	April (16-28)	92.9	171.4	459.3	611.0	-
	May (1-5)	-	389.8	547.4	-	-
	May (10-21)	-	414.5	700.4	579.0	495.9
	August	1279.1	939.6	-	-	-

(Fig. 4; Fig. 12). High carbon uptake rates were also observed at eddy stations occupied in the open ocean area (average $1300.1 \text{ mg C m}^{-2} \text{ day}^{-1}$). During June, ^{13}C uptake ranged from 28 to $1390 \text{ mg C m}^{-2} \text{ day}^{-1}$. The average vertically integrated carbon uptake rates were lower over the middle shelf ($122.2 \text{ mg C m}^{-2} \text{ day}^{-1}$) than the outer shelf ($292.7 \text{ mg C m}^{-2} \text{ day}^{-1}$). Along the 70m isobath transect the ^{13}C uptake rates were high around mooring 2 (M2) stations and decreased toward the north during June.

3.3.2 1998 ^{13}C uptake spatial distributions

In April, ^{13}C uptake rates ranged from 59.4 to $633 \text{ mg C m}^{-2} \text{ day}^{-1}$ over the Bering Sea shelf. The average vertically integrated uptake rates were lower in the middle shelf ($171.4 \text{ mg C m}^{-2} \text{ day}^{-1}$) than in the outer shelf ($459.3 \text{ mg C m}^{-2} \text{ day}^{-1}$) (Table 2). This pattern was similar to that observed in 1997. Along the 70m isobath transect carbon uptake rates showed a distribution similar to 1997 with high values around mooring 2 (M2) and decreasing toward the north. In May, ^{13}C uptake rates ranged from 52 to $1107.6 \text{ mg C m}^{-2} \text{ day}^{-1}$. The largest vertically integrated carbon uptake rate was observed at the innermost station of the middle shelf where strong fluorescence signals appeared. The average vertically integrated carbon uptake rates, however, were higher in the outer shelf ($700.4 \text{ mg C m}^{-2} \text{ day}^{-1}$) than in the middle shelf ($414.5 \text{ mg C m}^{-2} \text{ day}^{-1}$). The carbon uptake values at the shelf break and in the open ocean were $579.0 \text{ mg C m}^{-2} \text{ day}^{-1}$ and $495.9 \text{ mg C m}^{-2} \text{ day}^{-1}$, respectively.

3.4 Nitrogen uptake

3.4.1 1997 ^{15}N uptake spatial distributions

During May 1997, vertically integrated nitrate uptakes over the Bering shelf ranged from 8 to 917 $\text{mg N m}^{-2} \text{ day}^{-1}$. The average vertically integrated nitrate uptake over the middle shelf ($13.6 \text{ mg N m}^{-2} \text{ day}^{-1}$) was much lower than that over the outer shelf ($118.9 \text{ mg N m}^{-2} \text{ day}^{-1}$) and the open ocean ($433.0 \text{ mg N m}^{-2} \text{ day}^{-1}$) (Table 3). An early spring depletion of nitrate could explain the lower integrated nitrate uptake rates over the middle shelf compared with the outer shelf and open ocean areas. Most of the high nitrate uptake rates in the open ocean occurred at the shelf break and in eddy regions. Ammonium uptake rates ranged from 20 to 1545 $\text{mg N m}^{-2} \text{ day}^{-1}$. An average ammonium uptake rate over the middle shelf ($74.6 \text{ mg N m}^{-2} \text{ day}^{-1}$) corresponded to that of the outer shelf ($86.6 \text{ mg N m}^{-2} \text{ day}^{-1}$). Urea uptake rates ranged from 12 to 201 $\text{mg N m}^{-2} \text{ day}^{-1}$. The average urea uptake rate over the middle shelf ($30.8 \text{ mg N m}^{-2} \text{ day}^{-1}$) was much lower than over the outer shelf ($97.4 \text{ mg N m}^{-2} \text{ day}^{-1}$). High ammonium uptake rates occurred at one of the eddy stations and at a middle front station where high nitrate uptake rates were also observed. This implies that both stations were supplied with high nutrients, not only from the lower layer but also from active regeneration processes. An f-ratio was estimated using nitrate uptake rate/(nitrate + ammonium + urea) uptake rates. The f-ratios over the middle shelf, outer shelf, and shelf break were 0.16, 0.39, and 0.91, respectively. Thus nitrate is an important nitrogen source for phytoplankton in the outer shelf and shelf break regions.

During June 1997, vertically integrated nitrate uptake rates ranged from 2.1 to 143.5 $\text{mg N m}^{-2} \text{ day}^{-1}$. The integrated nitrate uptake rates were generally low and showed little spatial variation over the entire shelf region (Table 3). Average vertically

Table 3. Averaged vertically integrated nitrogen uptake rates over the Bering Sea shelf during 1997 and 1998 (mg N m⁻² day⁻¹).

Year	Date	Inner shelf				Middle shelf				Outer shelf				Shelf break			
		NO ₃	NH ₄	Urea	f	NO ₃	NH ₄	Urea	f	NO ₃	NH ₄	Urea	f	NO ₃	NH ₄	Urea	f
97	May	18.3	86.2	44.4	0.12	13.6	74.6	30.8	0.11	118.9	86.6	97.4	0.39	375.7	23.4	11.9	0.91
	June	6.6	-	-	-	4.5	73.4	41.4	0.04	5.7	157.1	68.4	0.02	13.2	299	42.5	0.04
98	April	-	-	-	-	7.4	54.8	-	0.12	18.1	64.2	-	0.22	33.4	96	-	0.26
	May(1-6)	-	-	-	-	10.0	486.9	-	0.02	20.7	821.4	-	0.02	-	-	-	-
	May	-	-	-	-	24.2	306.2	-	0.07	39.2	620.9	-	0.06	-	-	-	-
	August	19.7	496	-	-	5.1	156	-	0.03	-	-	-	-	-	-	-	-

integrated nitrate uptake rates over the middle shelf ($4.5 \text{ mg N m}^{-2} \text{ day}^{-1}$) were similar to those of the outer shelf ($5.7 \text{ mg N m}^{-2} \text{ day}^{-1}$). The similarity is most likely due to low nitrate concentrations in the water column over both areas (Fig. 10). Vertically integrated nitrate uptake rates in the middle shelf had little spatial variation. There were lower uptake rates around M2 and M4 stations with relatively high uptake rates at a mid-transect station along the 70 m isobath which had slightly higher nitrate concentrations in the deeper water column compared to both ends of the transect. High nitrate uptake rates (average $68.2 \text{ mg N m}^{-2} \text{ day}^{-1}$) were obtained at the first sampling of the eddy stations, but two weeks later the nitrate uptake rates had sharply decreased to $6.6 \text{ mg N m}^{-2} \text{ day}^{-1}$. The f-ratios measured during June 1997 over the middle shelf, outer shelf, and shelf break were 0.01, 0.02, and 0.04, respectively. This suggested that phytoplankton relied on regenerated nitrogen.

3.4.2 1998 ^{15}N uptake spatial distributions

During April 1998, nitrate uptake rates ranged from 2.3 to $33.4 \text{ mg N m}^{-2} \text{ day}^{-1}$. The average vertically integrated nitrate uptake rate over the middle shelf was slightly lower ($7.4 \text{ mg N m}^{-2} \text{ day}^{-1}$) than over the outer shelf region ($18.1 \text{ mg N m}^{-2} \text{ day}^{-1}$) (Table 3). Nitrate concentrations in the water column were high in both regions and may not have affected nitrate uptake rates. Ammonium uptake rates ranged from 25 to $96 \text{ mg N m}^{-2} \text{ day}^{-1}$. Average vertically integrated ammonium uptake rates over the middle shelf region ($54.8 \text{ mg N m}^{-2} \text{ day}^{-1}$) were similar to those over the outer shelf region ($64.2 \text{ mg N m}^{-2} \text{ day}^{-1}$). The outer shelf had higher nitrate uptake rates than the middle shelf but ammonium uptake rates were similar. The average f-ratio of the middle shelf (0.12), therefore, was lower than that of the outer shelf (0.22).

The May 1998 sampling consisted of two parts. During the first part (May 1-6, 1998), only mooring stations were occupied over the middle and the outer shelf. When compared with April 1998 values, vertically integrated nitrate uptakes were similar for both shelf areas, but vertically integrated ammonium uptake rates increased dramatically over both regions. The average f-ratios of the middle and outer shelves were 0.02 and 0.03, respectively. During the second cruise (May 6-22, 1998), vertically integrated nitrate uptake rates ranged from 11.9 to 64.2 mg N m⁻² day⁻¹. Generally, average vertically integrated nitrate uptake rates increased from the middle shelf (24.17 mg N m⁻² day⁻¹) toward the outer shelf (39.2 mg N m⁻² day⁻¹) and the open ocean (46.22 mg N m⁻² day⁻¹). But the highest nitrate uptake rate in the across shelf transect (17.8 mg N m⁻² day⁻¹) occurred at the most inner (i.e. coastal) station where the highest fluorescence also was observed. Nitrate uptake rates over both the middle and outer shelves were doubled compared to the preceding May 1-6 1998 cruise, while ammonium uptake rates decreased to about 37% of those observed during the May 1-6 1998 cruise over the middle shelf and also decreased 24% for the outer shelf. Ammonium uptake rates ranged from 22 mg N m⁻² day⁻¹ in the open ocean region to 636 mg N m⁻² day⁻¹ over the outer shelf. Average vertically integrated ammonium uptake for the middle shelf was lower (306.2 mg N m⁻² day⁻¹) than for the outer shelf region (620.9 mg N m⁻² day⁻¹). The open ocean region had the lowest average integrated ammonium uptake rate (22 mg N m⁻² day⁻¹). The average f-ratios of the middle and outer shelves were 0.08 and 0.06, respectively. The contribution of ammonium to phytoplankton growth decreased slightly as ammonium concentrations decreased.

4. DISCUSSION

During the PROBES project of the late 1970's and early 1980's studies were conducted on the interactions between the spring phytoplankton bloom over the Bering Sea continental shelf and water column physics and chemistry using ^{15}N -nitrogen uptake techniques (e.g., Sambrotto *et al.*, 1986; Sambrotto and Goering, 1983). It was found that wind mixing plays an important role in controlling not only the amount of nutrients available for phytoplankton growth but also light conditions in the water column. The initiation of the spring bloom over the southeastern Bering Sea shelf was shown to be closely related to the interruption of the wind mixing events caused by low pressure systems moving through the area. This hiatus of wind mixing occurred between late April and early May. The spring bloom over the middle shelf, therefore, commenced consistently during this period and reached peaks in mid-May during 1979, 1980, and 1981 (Sambrotto *et al.*, 1986).

The southeastern Bering Sea shelf region is relatively shallow and a large proportion of the shelf area experiences a seasonal advance and retreat of sea ice. It is also well known that the primary production over the southeastern Bering Sea shelf is influenced by the seasonal ice arrival and retreat in early spring (Alexander and Niebauer, 1981; Niebauer and Alexander, 1985; Niebauer *et al.*, 1990). As seasonal sea ice retreats, the melting provides cold and low salinity water to the initially high nutrient water and forms strong stratification and a shallow surface wind mixed layer. This initiates a phytoplankton bloom along the ice edge. In most years the ice edge bloom is short lived due to open water column wind mixing and the rapid consumption of nitrate by phytoplankton. After the spring storms bring nutrients into the surface layer

the more typical water column spring bloom occurs in late April-early May (Niebauer *et al.*, 1990). Therefore, the advance and retreat of seasonal sea ice greatly affects the seasonal distribution of the total annual primary production over the Bering Sea shelf through the occurrence of ice edge related phytoplankton bloom.

4.1 Changing bloom conditions during 1997 and 1998

4.1.1 1997 bloom sequence

As the 1997 sea ice retreated from the southeastern Bering Sea shelf, it experienced unusual atmospheric conditions - warm, clear skies, and absence of storms - that resulted from an anomalously high sea level pressure (SLP). The unusual atmospheric conditions continued through the summer period of 1997 which resulted in the strengthening of water column stratification over the southeastern Bering Sea shelf compared to other years (1995, 1996, and 1998) (Stabeno *et al.* 2000). These conditions allowed a sea ice-related bloom to develop during late April over the middle shelf area while the open ocean bloom driven by the thermal stratification, proceeded over the sea ice free outer shelf area.

Vertically integrated carbon and nitrogen uptake rates along with chlorophyll concentrations over the shelf water column in the presence of strong stratification indicated that peak bloom conditions were occurring over the outer shelf while post-bloom conditions prevailed over the middle shelf during 5-7 May 1997 (Fig. 4; Fig. 20; Fig. 21). During 1997, sea ice advanced to mooring 2 (M2) and persisted from mid March through early April (Fig. 2). During the PROBES years, nitrate uptake rates during the spring bloom periods were over $30 \text{ mg-at m}^{-2} \text{ day}^{-1}$ on the middle and outer

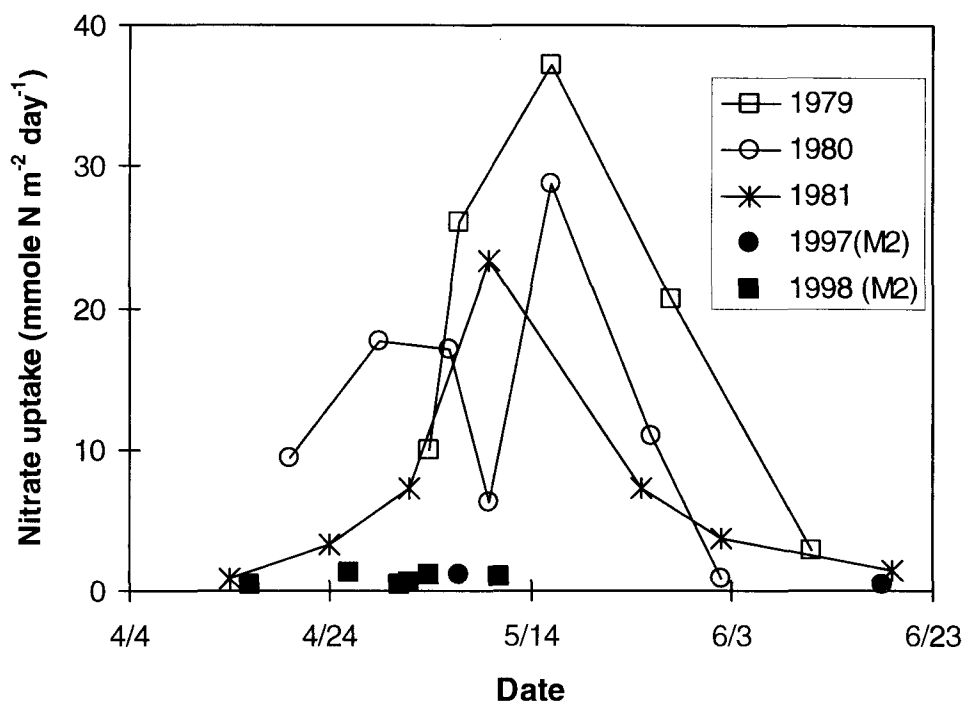


Fig. 20 Time series of integrated nitrate uptake rates ($\text{mmole N m}^{-2} \text{ day}^{-1}$) over the middle shelf area during PROBES (from Sambrotto et al. 1986) and this study.

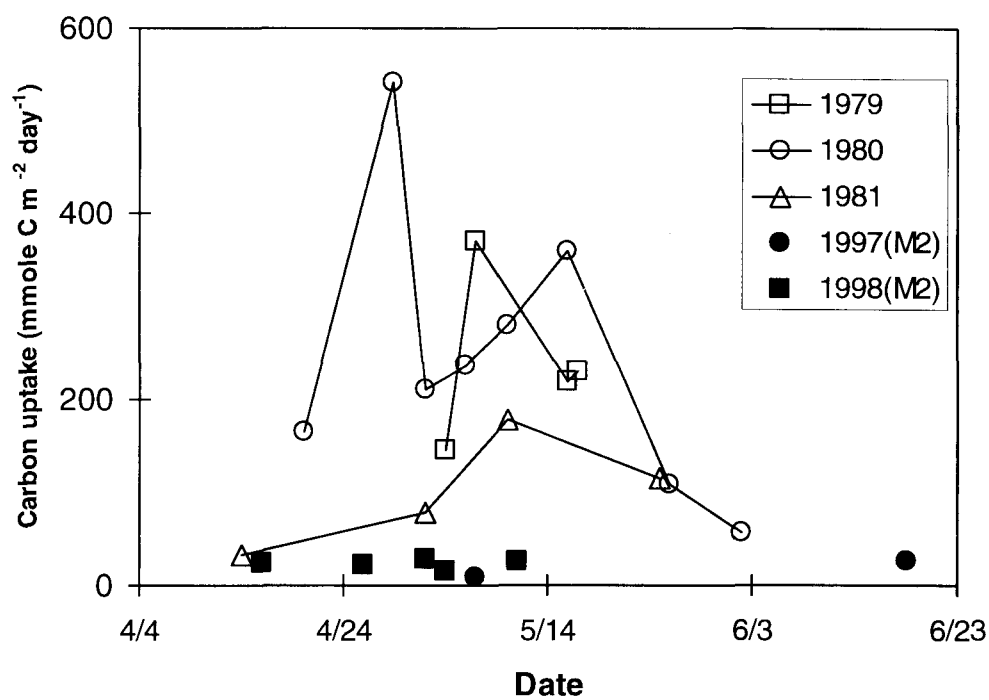


Fig. 21 Time series of integrated carbon uptake rates ($\text{mmole C m}^{-2} \text{ day}^{-1}$) over the middle shelf area during PROBES (^{14}C) (data from Sambrotto et al. 1986) and this study (^{13}C).

shelf areas (Sambrotto *et al.*, 1986). In early May, 1997, we observed a very low nitrate uptake rate ($1.1 \text{ mg-at m}^{-2} \text{ day}^{-1}$) at mooring 2 (M2) over the middle shelf, which approximates the nitrate uptake rate observed during the summer of 1997 ($0.2\text{-}0.7 \text{ mg-at m}^{-2} \text{ day}^{-1}$) over the entire shelf region. At mooring 3 (M3) over the outer shelf area the nitrate uptake rate was moderately high ($8.5 \text{ mg-at m}^{-2} \text{ day}^{-1}$), which is similar to the nitrate uptake rates observed just before the bloom peak during the PROBES years. Carbon uptake rates showed a trend similar to nitrate uptake rates (Fig. 21).

Nitrate concentrations in the euphotic layer should be a good indicator of water column phytoplankton blooms. Whitledge *et al.* (1986) described the annual cycle of nutrient concentrations over the southeastern Bering Sea shelf area during the PROBES years. The highest nitrate concentrations over the upper 40m at inner, middle, and outer shelf stations were observed from late April to early May on the PROBES main station line, stations similar to the ones occupied in this study. As the spring bloom occurred in May nitrate concentrations of the middle shelf declined rapidly to $< 1 \mu\text{M}$ at the beginning of June. In early May 1997, nutrients (especially, nitrate and silicate) were already depleted in the whole water column over the middle shelf area and in the surface layer ($< 50\text{m}$) of the outer shelf region (Fig. 9). Integrated nitrate content was similar to that observed at the end of the spring bloom during the PROBES project (Fig. 22).

After the spring bloom, phytoplankton usually sink into deeper water because of the depletion of nitrate in the euphotic layer. In early May 1997, chlorophyll concentrations were very low over the upper water column at the middle shelf mooring 2 (M2) ($< 0.1 \mu\text{g Chl l}^{-1}$) and showed small increases with depth ($0.24 \mu\text{g Chl l}^{-1}$). High chlorophyll concentrations were observed at mooring 3 (M3) over the outer shelf

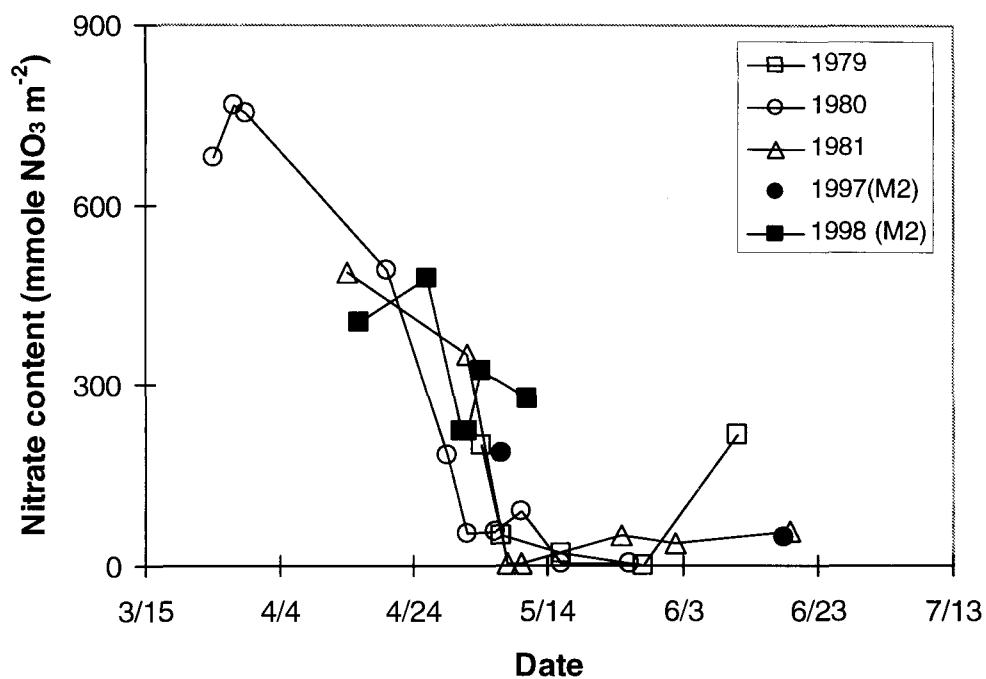


Fig. 22 Time series of integrated nitrate (mmole $\text{NO}_3 \text{ m}^{-2}$) over the middle shelf area during PROBES (data from Sambrotto et al. 1986) and this study

(> 5 $\mu\text{g Chl l}^{-1}$) (Fig. 23).

The C/N (atom:atom) ratios of particulate matter also give clues to the status of the phytoplankton bloom. The C/N ratios in particulate matter are low during the stable and peak bloom periods compared to pre-bloom and post-bloom periods. This occurs because nitrogen assimilation rates are maximal, while carbon assimilation rates are actually lower than during the pre bloom and post bloom periods. High C/N compositional ratios were found during a vigorous mixing event and during post bloom periods in the southeastern Bering Sea middle shelf region in 1980 (Sambrotto, 1986). Landing and Feely (1981) also observed a high C/N (> 10) in the particulate material collected before stabilization in the northwestern Gulf of Alaska. The C/N ratio of particulate material was high (10.5) at mooring 2 (M2) and was low (4.5) at mooring 3 (M3) during May 1997. Thus, the middle shelf area was experiencing low nitrate concentrations while the outer shelf area had sufficient nitrate for phytoplankton growth. During June 1997, high C/N ratios of particulate material were also observed over the shelf area.

Generally, during the PROBES studies a high f-ratio was observed during the spring bloom period due to the high concentration of nitrate and active uptake of nitrate by phytoplankton. However, during post bloom periods the f-ratios decreased significantly and the nitrogen demands of phytoplankton communities were met by regenerated nitrogen such as ammonium and urea (Sambrotto, 1986). During May 1997, the f-ratio was moderate over the outer shelf (0.39) and was low over the middle shelf (0.11).

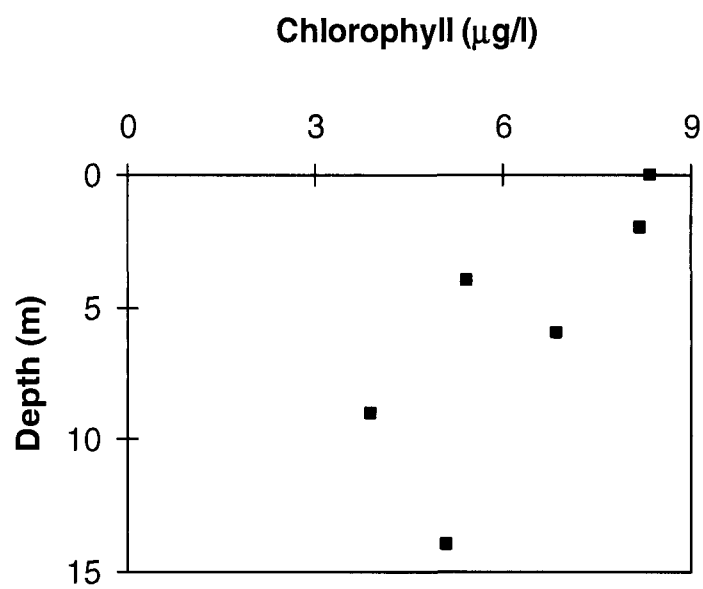
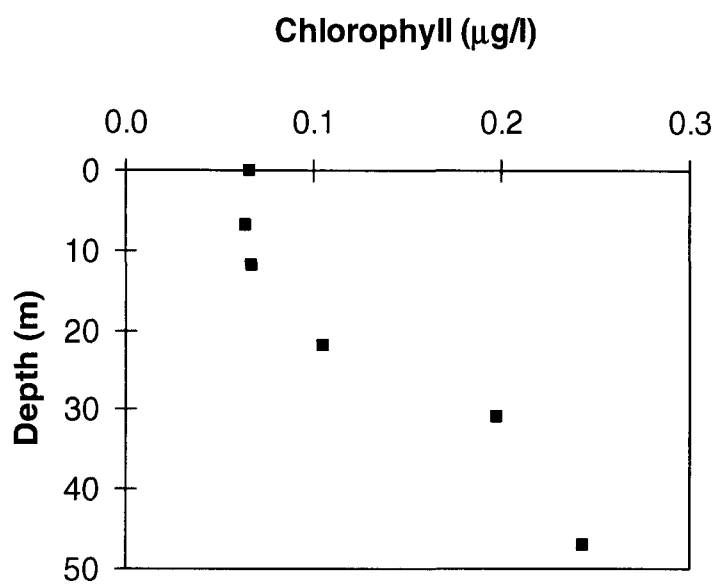


Fig. 23 Chlorophyll concentrations at mooring 2 (M2) (upper) and mooring 3 (M3) (lower) during May 1997.

4.1.2 1998 bloom sequence

In 1998, another unusual bloom sequence was observed. During the early spring (April and May) of 1998 storm events were more frequent than usual and strong winds mixed the water column homogeneously over the southeastern Bering Sea shelf area (Stabeno *et al.*, 2000). These events brought nutrient-rich slope water to the shelf region and prevented the establishment of stratification an essential factor for bloom development (Fig. 8; Fig. 9; Fig. 16; Fig. 17). The typical spring water column bloom, therefore, did not develop. Phytoplankton, however, utilized the nitrate in the water column slowly. Low carbon and nitrate uptake rates were observed during both April and May cruises. Nitrate concentrations over the middle shelf area were $> 12 \mu\text{M}$ during the early April cruise and decreased to $> 8 \mu\text{M}$ during the mid May cruise. Vertically integrated carbon uptake rates at mooring 2 (M2) ranged from $294.2 \text{ mg C m}^{-2} \text{ day}^{-1}$ during early April 1998 to $389.75 \text{ mg C m}^{-2} \text{ day}^{-1}$ during early May and $322.5 \text{ mg C m}^{-2} \text{ day}^{-1}$ during middle May. These rates were similar to the values observed at the end of the 1997 spring bloom ($186.9 \text{ mg C m}^{-2} \text{ day}^{-1}$) or during the summer ($417.9 \text{ mg C m}^{-2} \text{ day}^{-1}$) over the middle shelf. The nitrate uptake rates were $12 \text{ mg N m}^{-2} \text{ day}^{-1}$, $10 \text{ mg N m}^{-2} \text{ day}^{-1}$, and $13.5 \text{ mg N m}^{-2} \text{ day}^{-1}$, during early April, early May, and mid May of 1998, respectively. These were slightly higher than the summer rates ($2.6 \text{ mg N m}^{-2} \text{ day}^{-1}$) obtained during June 1997.

However, the ammonium uptake rates were substantially different from nitrate uptake rates among years. The C/N ratio of particulate materials in 1998 was higher (> 8) than that expected from the Redfield ratio (6.6) but lower than in 1997, due partly to the high ammonium uptake during 1998. The ammonium uptake rates were 72.9 mg N

$\text{m}^{-2} \text{ day}^{-1}$ during early April 1998 and increased sharply to $440.8 \text{ mg N m}^{-2} \text{ day}^{-1}$ and $350 \text{ mg N m}^{-2} \text{ day}^{-1}$ during early May and mid May, respectively. A large increase in ammonium concentrations in the water column probably resulted in the observed large increases of ammonium uptake. At mooring 3 (M3), vertically integrated carbon uptake rates were $285.1 \text{ mg C m}^{-2} \text{ day}^{-1}$ during early April 1998 and continuously increased to $547.4 \text{ mg C m}^{-2} \text{ day}^{-1}$ and $784.6 \text{ mg C m}^{-2} \text{ day}^{-1}$ during early May and mid May, respectively. Ammonium uptake rates showed a trend similar to that observed at mooring 2 (M2).

The f-ratio for 1998 was calculated as [nitrate uptake rate/(nitrate + ammonium) uptake rate] because urea uptake rates were not available. During early April 1998, even though nitrate concentrations were high, the f-ratios were 0.2 and 0.29 at mooring 2 (M2) and mooring 3 (M3), respectively. The f-ratios would be lower if urea uptake were included in the calculation. Hansell *et al.* (1989) showed that the f-ratio increases about 25% when it is calculated from only nitrate and ammonium uptake rates.

The extensive wind mixing of the water column continued through the spring and early summer of 1998 and produced conditions that allowed an extended phytoplankton growing season due to the continuous supply of nitrate from the nutrient-rich slope water (Stabeno *et al.*, 2000). According to the fluorescence data recorded at mooring 2 (M2) (Stabeno *et al.*, 2000), the fluorescence signal increased in mid May. We do not have carbon and nitrate uptake data because we arrived at mooring 2 (M2) on May 11, 1998, just before the increase. However, the carbon uptake rates increased gradually from $322.5 \text{ mg C m}^{-2} \text{ day}^{-1}$ at mooring 2 (M2) to $525.8 \text{ mg C m}^{-2} \text{ day}^{-1}$ and $1107.6 \text{ mg C m}^{-2} \text{ day}^{-1}$ at stations 32 and 33 (located inshore of mooring 2 (M2)). Nitrate and ammonium uptake rates showed trends similar to carbon uptake. During the PROBES years the

bloom began first over the outer shelf and then moved into the middle and inner shelf (Whitledge, 1986). The carbon and nitrate uptake data imply that the spring increase of phytoplankton in 1998 occurred first in the inner shelf.

4.2 Unusual deep nitrate uptake

During May 1997 nitrate concentrations were depleted the upper layer and remained high below the pycnocline, similar to observations during the PROBES studies (Fig. 24). During summer 1997 the southeastern Bering Sea shelf experienced an unusual depletion of the nitrate pool ($< 5 \mu\text{M}$) below the pycnocline over the middle shelf (Fig. 25) (Stockwell *et al.*, submitted). However, in 1998 high nitrate concentrations were observed until late May throughout the entire water column over the middle shelf (Fig. 24). Physical and biological processes play an important role in controlling nitrate concentrations (Sambrotto *et al.*, 1986; Whitledge *et al.*, 1986). The seasonal cycle of nitrate over the southeastern Bering Sea shelf was well quantified during the PROBES project of the late 70's and early 80's. From late summer through winter nitrate concentrations over the middle and outer shelf were replenished and attained maxima before the initiation of the spring phytoplankton bloom. After the spring bloom nitrate was depleted over the upper 40m but remained at relatively high concentrations (8 to 10 μM) below the pycnocline over the middle shelf (Whitledge *et al.*, 1986).

During the PROBES years nitrate concentrations gradually increased from fall through winter and early spring over both the middle and outer shelf. This suggested that nutrients were not flushed on shelf by an abrupt advection event but were replenished in the upper layer by the slow erosion of the bottom layer by vertical wind mixing. It was believed that nitrate was brought into the outer and middle shelf region by tidally driven

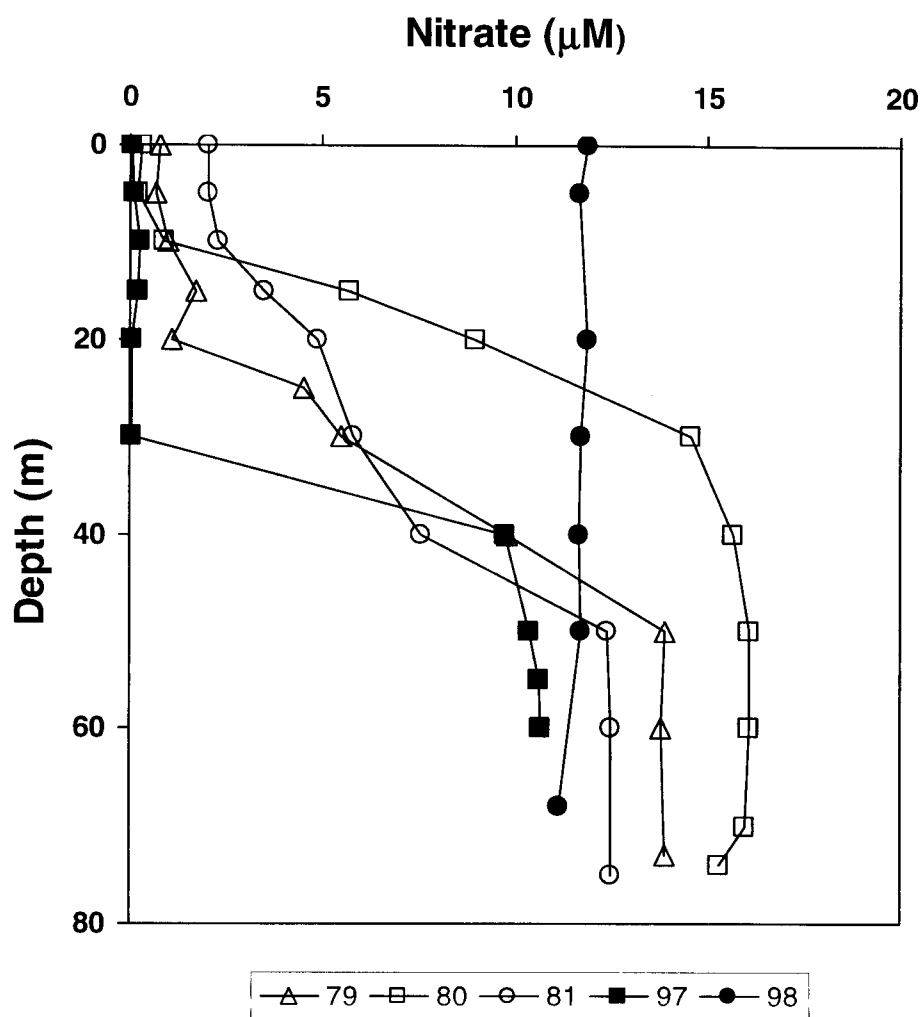


Fig.24 Vertical nitrate concentration profiles over the middle shelf during May of the PROBES years (1979,1980, and 1981) and this study (1997 and 1998).

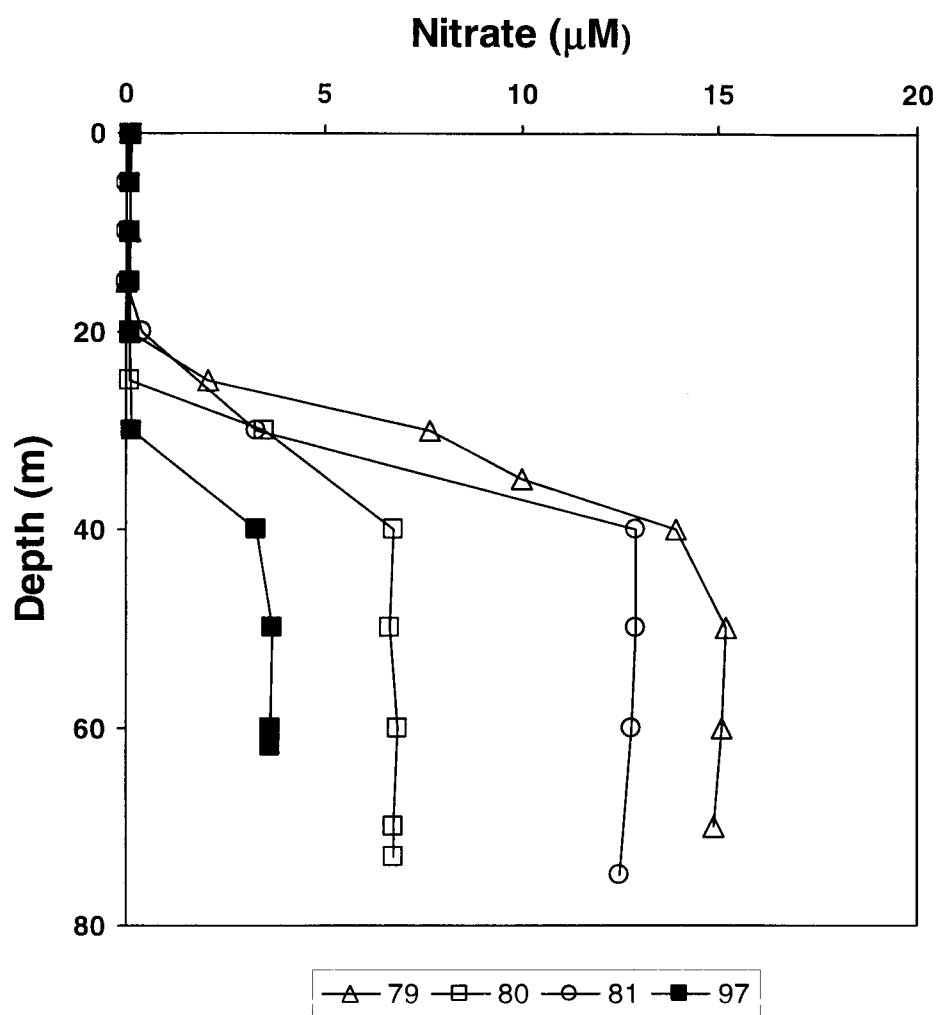


Fig.25 Vertical nitrate concentration profiles over the middle shelf during June of the PROBES project (1979,1980,and 1981) and 1997.

cross-shelf diffusion the lack of strong currents in the middle shelf and the presence of a strong frontal system, which retarded the horizontal advection of nutrients from offshore (Coachman and Walsh, 1981; Whitley *et al.*, 1986).

During the SEBSCC study, however, the monthly mean current data suggested that onshelf flow could be an important factor in replenishing the nutrients and salts over the middle shelf. During 1997 the weak mean currents evident in the satellite-tracked drifting buoy data, resulted in a relative lack of advection of high nutrient slope water onto the middle shelf. Therefore, deep nitrate concentrations, reduced by a strong storm mixing event in late May, did not recover to the typical concentrations (8 -10 μM) expected from the PROBES study. However, the frequent storms and strong winds during winter and spring 1998 produced stronger currents than average on the middle shelf resulting in a strong cross shelf transport of nutrients and salts (Stabeno *et al.*, 2000).

As pointed out earlier, phytoplankton blooms during early spring play a key role in regulating nutrient concentrations in the euphotic layer. Generally, nitrate uptake rates show a surface and/or a subsurface maximum and decrease with depth due to light limitation. In eutrophic regions nitrate uptake rates in the euphotic layer are limited by nitrate concentrations at the surface and by light intensity at the bottom (MacIsaac and Dugdale, 1972). Unusual conditions occurred over the Bering shelf that altered biological processes during June 1997. The unusual atmospheric conditions over the southeastern Bering Sea shelf - cloud free skies and reduced wind mixing - resulted in a shallow upper wind-mixed layer. This allowed the euphotic zone to extend below the pycnocline and enabled the phytoplankton to assimilate nitrate below the pycnocline. Nitrate specific uptake rates over the middle shelf increased with depth below the

pycnocline (Fig.26). Sambrotto (1983) reported that the phytoplankton living within the deep euphotic layer were better adapted to low light conditions by having a lower light half saturation constant, K_L , than those residing in the upper euphotic zone. These phytoplankton, thus, probably effectively assimilate nitrate at greater depths. In April and May 1998, nitrate uptake rates showed a more typical pattern with high rates at the surface and decreased rates with depth due to light limitation. Nitrate was abundant at all euphotic zone depths. Thus, nitrate concentrations did not regulate uptake (Fig. 13; Fig. 14).

In summary, an unusual response of nitrate uptake to a shallower pycnocline during the summer of 1997 allowed phytoplankton to assimilate nitrate throughout the water column. This resulted in the depletion of the deep nitrate pool below the pycnocline over the middle shelf area. During the winter and spring of 1998, strong wind mixing events resulted in unfavorable conditions for phytoplankton blooms and extended the 1998 growing season, due to a slowed depletion of nitrate.

4.3 Carbon and nitrogen uptake during the coccolithophorid bloom

Unusual atmospheric and oceanic conditions resulted in an unprecedented coccolithophorid bloom over the southeastern Bering Sea shelf during 1997. The bloom organism, *Emiliana huxleyi*, is small (approximately 10 μm diameter) and is covered with calcium carbonate platelets or coccoliths. Its small size means that it is likely to be consumed by microzooplankton, as well as copepods or euphausiids, which may result in a less efficient food chain leading to the upper trophic levels (Hunt *et al.*, 1999). The bloom was first observed by its effect on water color in early July 1997. In September the areal extent was documented with the first available SeaWiFS ocean

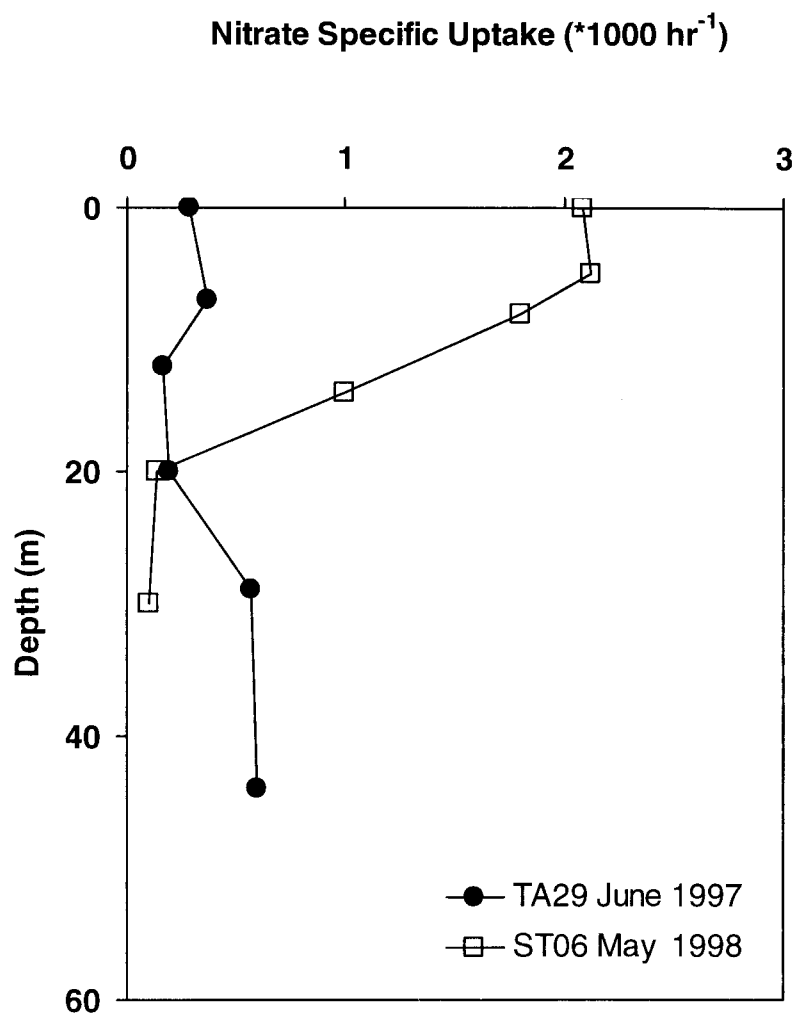
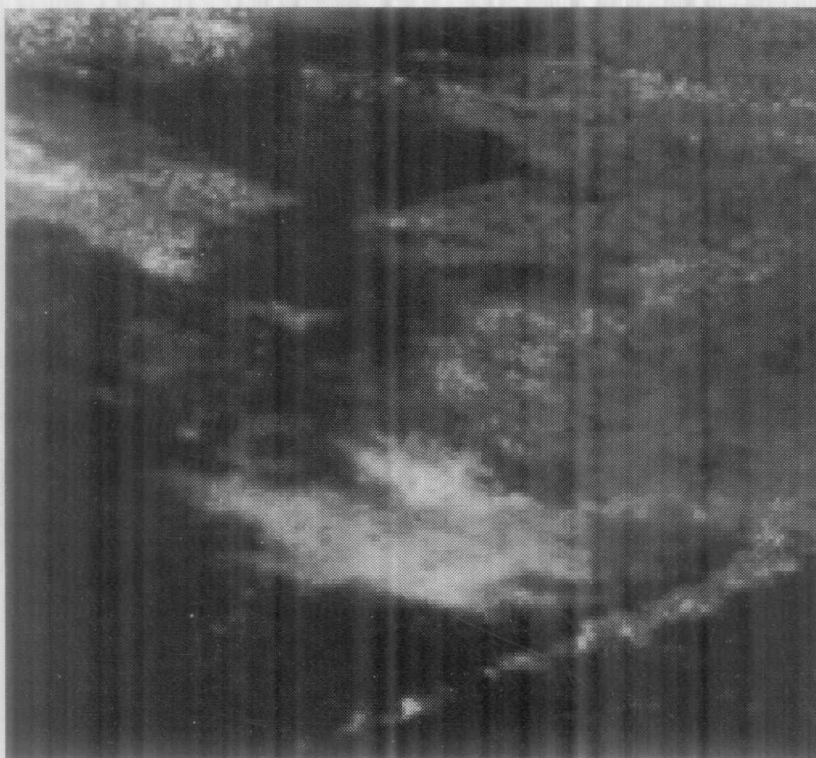


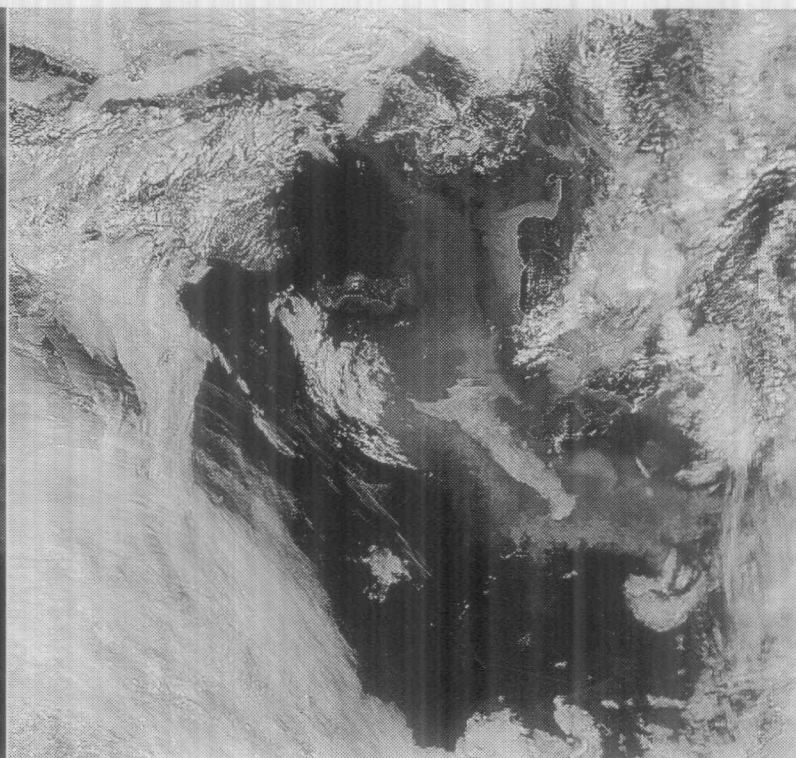
Fig.26 Nitrate specific uptake rates at mooring 2 (M2) (middle shelf) during June 1997 and May 1998.

color satellite images. During late September the bloom was ca. 700×300 km, and extended south from the Alaska Peninsula north to Nunivak Island and east from Bristol Bay to just west of the Pribilof Islands (Fig. 27) (Vance *et al.*, 1998). This outbreak continued through 1998 (Hunt *et al.*, 1999) and 1999.

Although we don't have an exact answer as to what factors allowed the coccolithophorid bloom to develop during 1997 and continue during 1998 and 1999, there are some plausible explanations. Diatoms are responsible for the major portion of "new" production over the southeastern Bering Sea shelf (Sambrotto *et al.*, 1986). Generally, large phytoplankton such as diatoms have high K_s values for nutrient uptake and large values of V_{max} . Thus, diatoms normally dominate when nutrients (nitrate and silicate) are abundant in the euphotic zone, and they can produce large amounts of organic material that will be grazed or exported out of the euphotic zone. However, small phytoplankton such as coccolithophorids and *Phaeocystis* spp., which have lower K_s values for nutrient uptake and low values of V_{max} , have a growth advantage in low nutrient regimes. A change of species composition was observed after the spring bloom over the Bering Sea shelf during the previous studies in the late 70's and early 80's but there are no reports of coccolithophorid blooms. The unusual conditions during 1997 — low cloud cover and low wind mixing — allowed a strong stratification of the wind mixed layer and led to high surface temperatures. Primary production in the presence of such strong stratification depleted both nitrate and silicate over the inner and middle shelves. These conditions may have been responsible for the observed change of species composition over the southeastern Bering Sea shelf (Stabeno *et al.*, 2000, Stockwell *et al.*, submitted). Egge and Heimdal (1994) reported that *E. huxleyi*, in mesocosm studies, showed a better adaptation to high temperature than *Phaeocystis* spp.



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Fig. 27 SeaWiFS color images of the southeastern Bering Sea Shelf coccolithophorid bloom during 1997 and 1998 ([Http:// rho.pmel.noaa.gov/~vance/seawifs/bering.html](http://rho.pmel.noaa.gov/~vance/seawifs/bering.html)).

Carbon and nitrogen uptake experiments during the coccolithophorid bloom were conducted in 1997 and 1998. The non-coccolithophorid dominated community showed higher carbon and nitrate specific uptake rates than the coccolithophorid dominated community, even though nitrate concentrations of waters of non-coccolithophorid dominated communities were low. The ammonium specific uptake rates of the coccolithophorid dominated bloom were higher than those of the non-coccolithophorid dominated bloom (Fig. 28). Therefore, the coccolithophorid dominated bloom probably depended more on ammonium than nitrate as a nitrogen source. Most of the coccolithophorid bloom region had high ammonium concentrations ($> 3 \mu\text{M}$) while the nitrate concentration was variable and had a wide range ($0.1 - 10.8 \mu\text{M}$). During early April and mid May 1998, there were large numbers of coccolithophorid cells in the water column over the southeastern Bering Sea shelf (Hunt *et al.*, 1999). The water column conditions remained relatively constant except for a small increase in temperature during this period (Fig. 13; Fig. 14). Nitrate and ammonium specific uptake rates were low during early April 1998. During mid May, the ammonium concentrations and ammonium specific uptake rates increased significantly, while the nitrate specific uptake rate increased slightly and nitrate concentrations decreased. Along with the higher temperature, high ammonium concentrations in the water column may be one of the more important factors regulating coccolithophorid blooms.

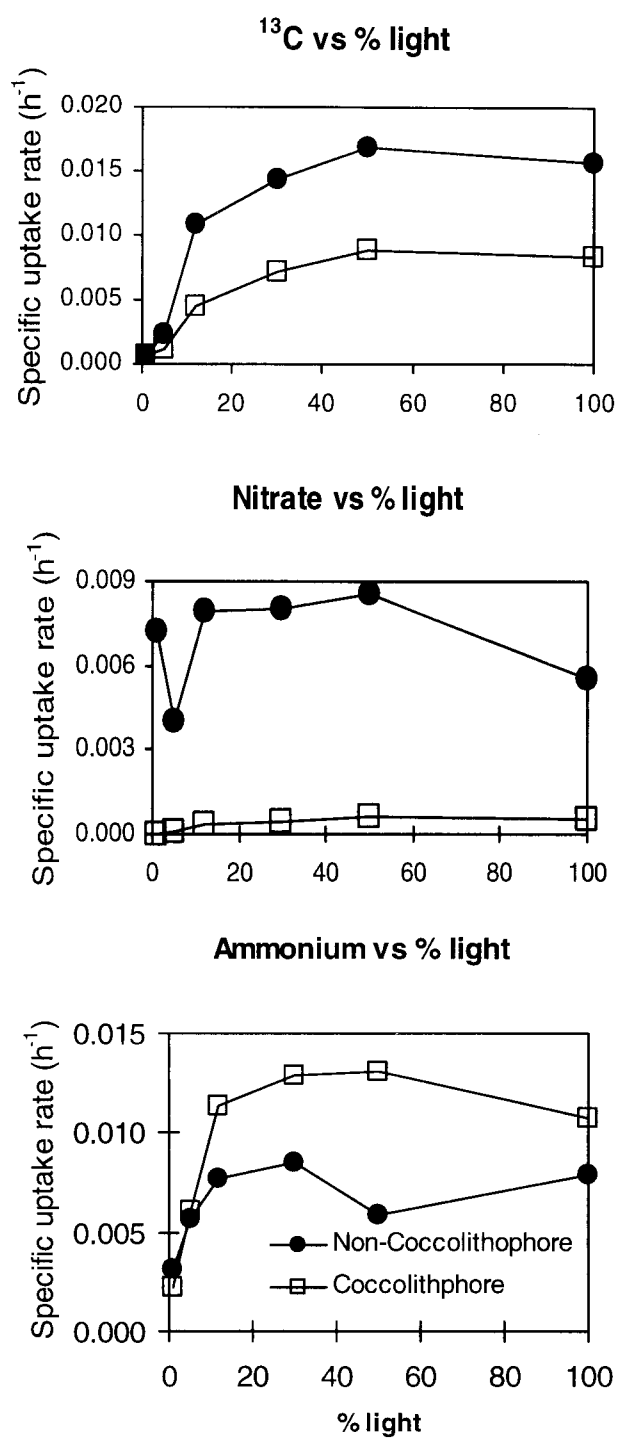


Fig. 28 Carbon, nitrate, and ammonium specific uptake rates (h^{-1}) of coccolithophorid bloom (NICX8 August 1998) and non-coccolithophore stations (St. 68 May 1997).

4.4 General ecosystem effects of the unusual Bering Sea shelf conditions during 1997 and 1998

During 1997 and 1998, unusual climatic conditions caused dramatic changes in the regional oceanic environment and greatly affected the function of the southeastern Bering Shelf ecosystem. In 1997, ice cover did not differ greatly from average, the northward retreat of sea ice was rapid, cloud cover was diminished, and storm events were less frequent. The lack of major wind events and reduced cloud coverage over the southeastern Bering Sea shelf were conspicuous features for both spring and summer, 1997. These conditions allowed the initial strong stratification, produced by melting ice, to persist and resulted in an earlier than normal spring bloom over the middle shelf. The ice related early bloom occurred before zooplankton were ready to harvest the phytoplankton in the water column (Niebauer *et al.*, 1990). The phytoplankton bloom, thus, probably escaped extensive grazing by zooplankton and settled to the bottom layer. The combined effects of reduced winds and cloud coverage during spring and summer of 1997 resulted in a low rate of the renewal of nitrate to the surface layer. The lack of nitrate renewal resulted in low "new" production in the surface layers of the euphotic zone over the middle shelf. Sambrotto and Goering (1983) reported that wind-induced mixing of nutrient-rich water from below the pycnocline into the euphotic zone, after termination of the spring bloom peak, increased annual primary production by as much as 30% in the southeastern Bering Sea shelf.

A sharp change of zooplankton abundance due to decoupling of the pelagic food chain and reduced "new" production was thus expected in 1997 over the middle shelf. However, no sharp change in the abundance and composition of the dominant

zooplankton species of the middle shelf was reported, although there were significantly lower densities of adult euphausiids in and around the inner front region (Napp *et al.*, 1999). The unusual conditions in 1997 allowed deep nitrate uptake to occur below the pycnocline and resulted in nitrate depletion in the deep nitrate pool over the middle shelf. This "new" production below the pycnocline resulted from phytoplankton growing at deep water depths. Thus, zooplankton over the middle shelf may not have experienced a dramatic change in the amount of food available for their consumption. The inner shelf region, however, may not have had enough nitrate in the lower layer to support the deep nitrate uptake needed for the post-bloom food demands of zooplankton.

The spring bloom of the southeastern Bering Sea shelf in 1998 exhibited a much different pattern than was observed in either 1997 or during the PROBES studies in the late 70's and early 80's. Greater amounts of nitrate were available to the phytoplankton because large amounts of nutrients were advected into the middle shelf due to the stronger than average currents (Stabeno *et al.*, 2000). McCarthy *et al.* (1977) used the relative preference index of nitrate (RPI_{NO_3}), ratio of % nitrate uptake to % nitrate concentration, to describe the uptake of a specific nutrient relative to its ambient concentration. If the RPI_{NO_3} is less than one, it indicates that phytoplankton utilized nitrate more slowly than would be anticipated from its availability. The nitrate uptake rates and relative preference index of nitrate (RPI_{NO_3}) suggested that phytoplankton assimilated nitrate slowly in 1998 compared to the availability of nitrate (Fig. 29; Fig. 30; Table. 4). During May and June 1997, nitrate concentrations in the surface euphotic zone were depleted. Nitrate uptake rates were low but showed high uptake rates where relatively high nitrate concentrations occurred (shelf break stations). During April and

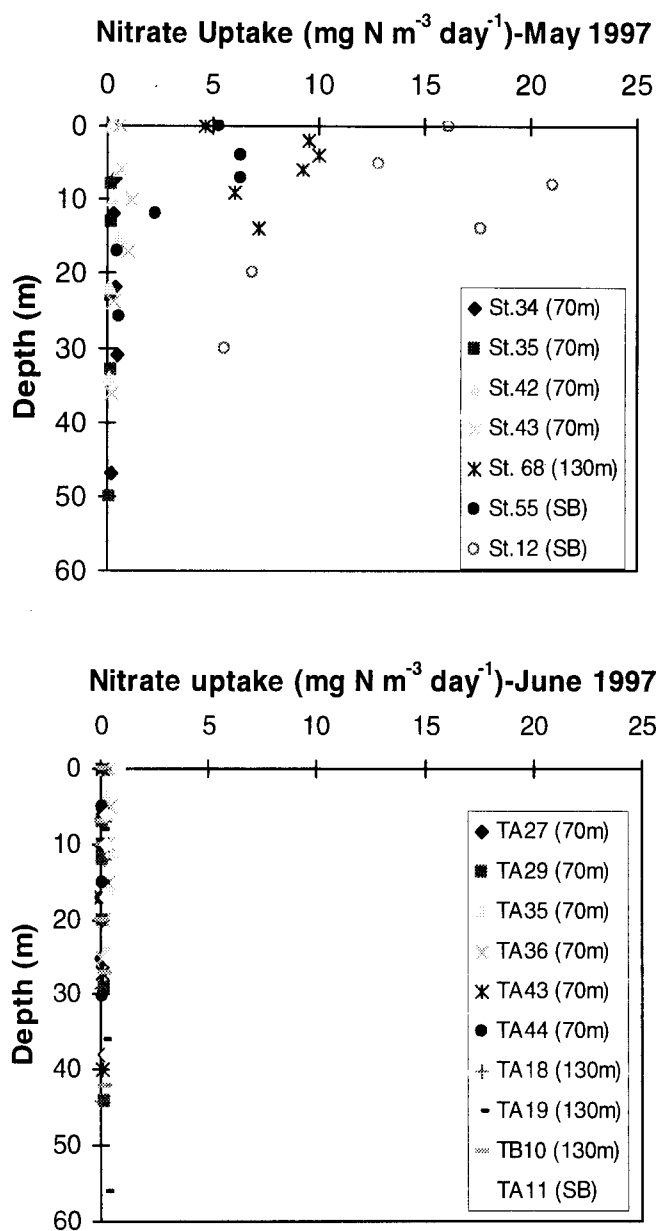


Fig. 29 Nitrate uptake rates over the southeastern Bering Sea shelf and shelf break (SB) during 1997.

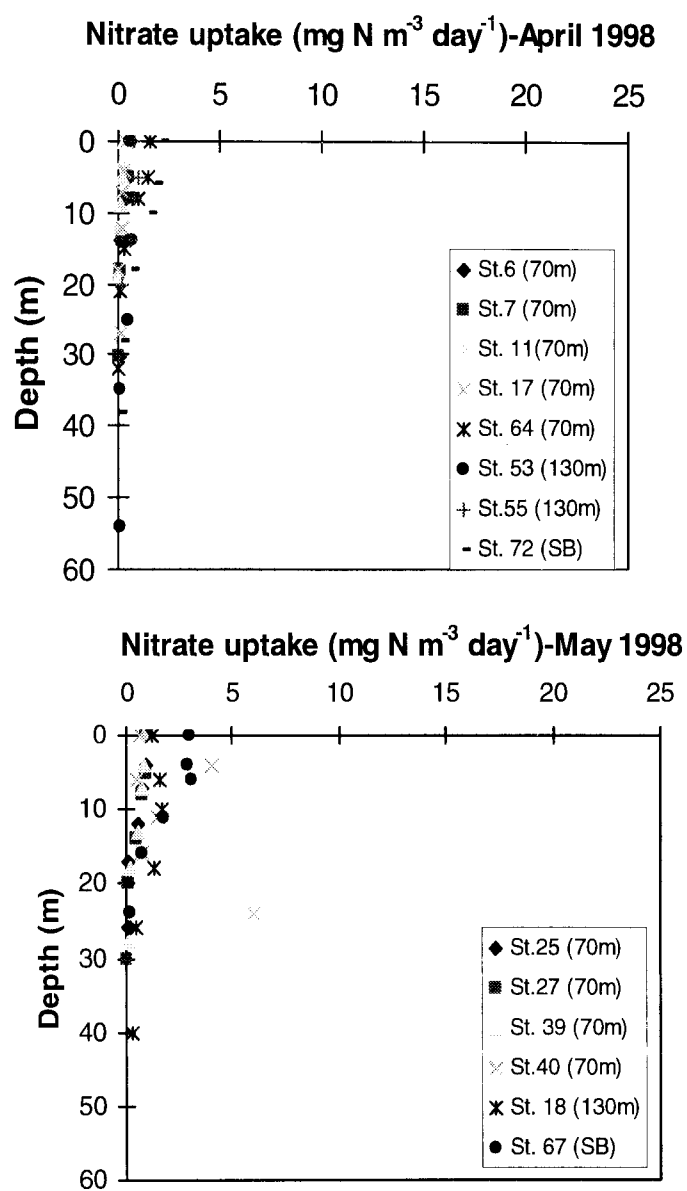


Fig. 30 Nitrate uptake rates over the southeastern Bering Sea shelf and shelf break (SB) during 1998.

Table 4. Relative Preference Index of nitrate (RPI_{NO_3}) over middle and outer shelf during 1997 and 1998. RPI_{NO_3} was averaged at 100% and 50% light depths to eliminate light effects on nitrate uptake rates.

Year	Date	Middle shelf (Mooring 2)	Outer shelf (Mooring 3)
1997	May	0.45	1.95
	June	0.24	0.12
1998	16 April	0.24	0.36
	26 April	0.44	-
	2 May	0.07	0.07
	10 May	0.10	0.07

May 1998, nitrate concentrations were high, but nitrate uptake rates were near those of 1997, when nitrate was depleted.

There are several possible factors to explain the observed lower than expected nitrate uptake rates when nitrate concentrations are high. First, because of the enhanced wind mixing during 1998 phytoplankton did not have favorable light conditions for rapid uptake of nitrate. During the first nitrogen uptake measurement of April 1998 at mooring 2 (M2) (April 16 1998), nitrate concentrations were high (ca. 13.4 μM) throughout the water column and ammonium concentrations were also high (ca. 2.5 μM), but nitrate uptake rates were near those observed during May 1997, and ammonium specific uptake rates were also low. During the second measurement (April 26 1998) at mooring 2 (M2), nitrate concentrations had slightly increased to ca. 15 μM and ammonium concentrations had decreased to ca. 0.7 μM . Nitrate specific uptake rates significantly increased while ammonium specific uptake remained the same as on April 16, 1998 (Fig. 31). The temperature and sigma-t profiles showed slight stratification on April 26, 1998 (Fig. 32).

Second, inhibition of nitrate uptake by high ammonium concentrations in the water column may be another reason for the observed low nitrate uptake despite high nitrate concentrations. On May 2, 1998, nitrate concentrations had decreased slightly compared to April 26 values, but ammonium concentrations had significantly increased (ca. 14 μM). The water column was also completely mixed and temperatures were ca. 2.1 °C. Nitrate specific uptake rates had markedly decreased compared to those of April 26, 1998. Although poor light conditions due to severe mixing may have been

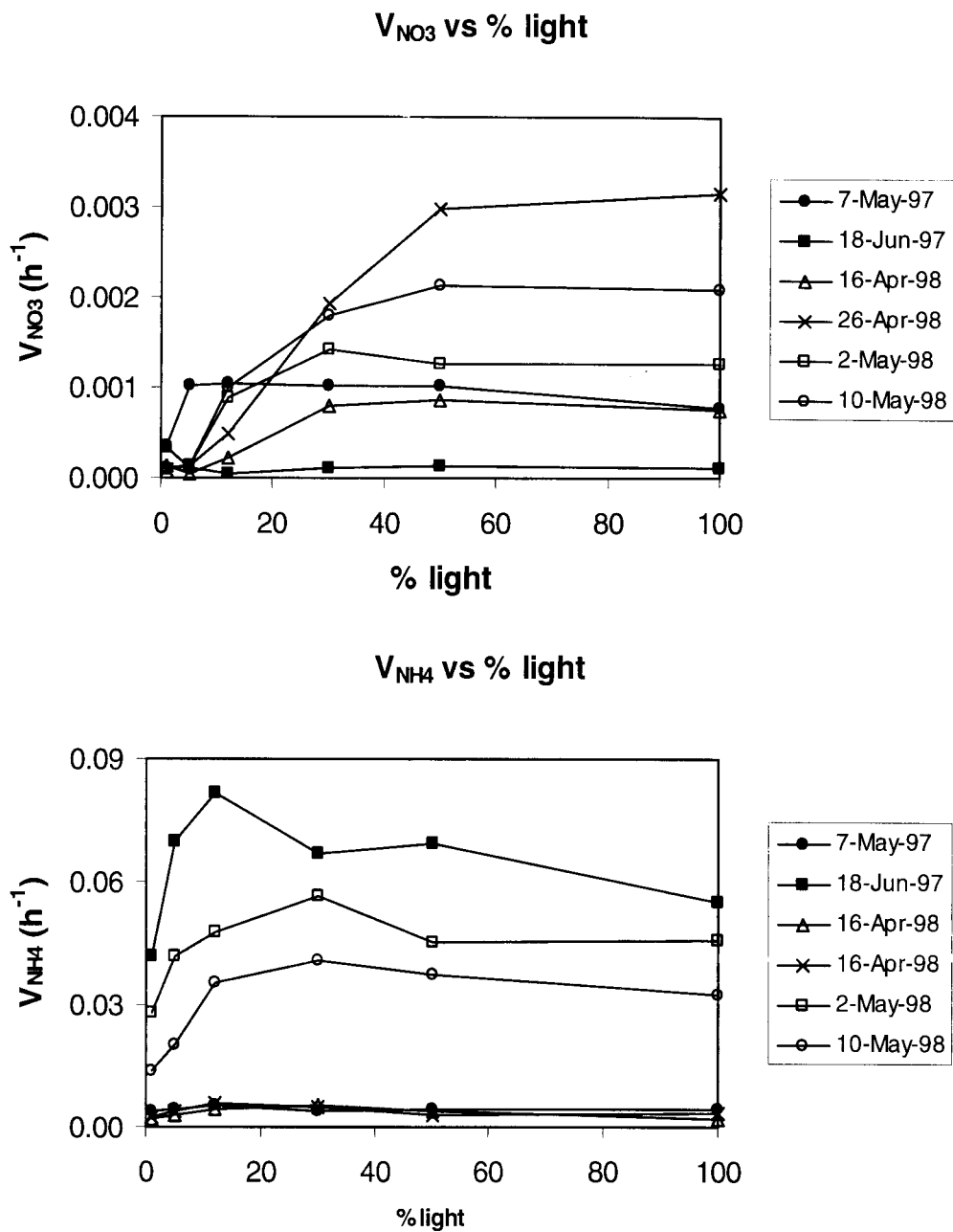


Fig. 31 Nitrate specific uptake rates vs. % light (upper) and ammonium specific uptake rates vs. % light (bottom) at mooring 2 (M2) over the middle shelf during 1997 and 1998.

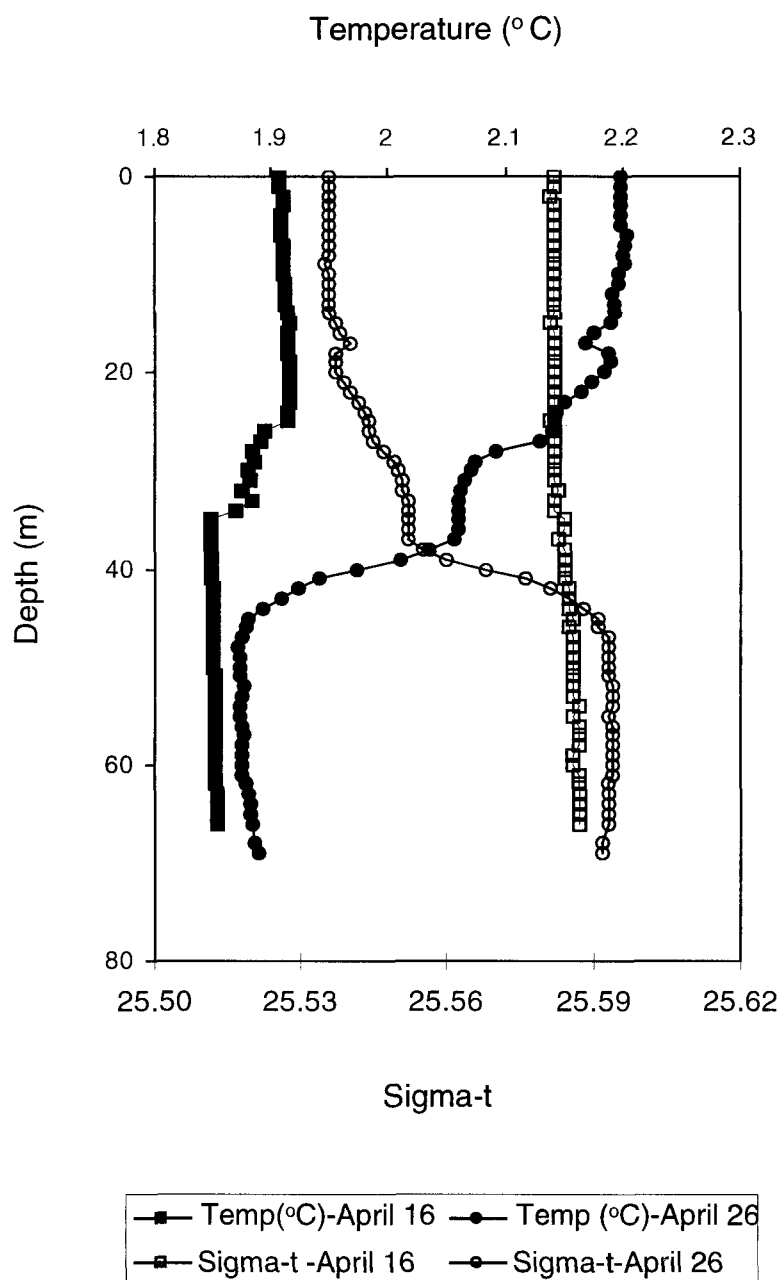


Fig. 32 Vertical distribution of temperature (closed) and sigma-t (open) at Mooring 2 over the middle shelf on April 16 (squares) and April 26 (circles) 1998.

responsible for the decrease in nitrate uptake, high ammonium concentrations and high ammonium specific uptake rates also cannot be ignored. On May 10, the water column conditions were completely mixed and temperatures were about 2.35 °C. Nitrate had decreased to ca 9.2 μM and ammonium also had decreased to ca. 5.2 μM throughout the water column. Ammonium specific uptake rates were slightly decreased and nitrate specific uptake rates were slightly increased compared to those on May 2. This indicated that high ammonium concentrations may have affected the nitrate uptake rates.

Third, elevated water column temperatures may have affected nitrate uptake rates over the southeastern Bering Sea shelf during 1998. Lomas and Glibert (1999) suggested that an increase in temperature resulted in a decrease in nitrate uptake rate and an increase in ammonium and urea uptake rates. Their results were obtained from nitrate uptake kinetics and direct short-term temperature manipulation studies on diatom-dominated field populations from Chesapeake and Delaware Bays, during both spring and fall blooms. Their temperature range was 7-25 °C.

All of the factors discussed above are possibly contributory. However, the temperature effect may be more important in causing the low nitrate uptake rates because high water temperatures can accelerate the remineralization of organic matter and thus directly increase ammonium concentrations. A temperature increase will also elevate ammonium concentrations indirectly through an increase in zooplankton metabolism (Smith and Vidal, 1986).

During 1997 and 1998, although the southeastern Bering Sea shelf experienced distinctively different mechanisms of primary production due to the unusual atmospheric-sea ice-ocean coupling, the amount of "new" production over the middle shelf may have

increased over the long term annual average due to deep nitrate uptake (1997) and protracted phytoplankton growth on the continuous supply of nitrate resulting from increased cross shelf transport (1998). The estimates of nitrate utilization, resulting from a "diagram analysis" over the 1997 and 1998 middle shelf spring bloom demonstrated "new" production to be similar for both years (Table 5). These estimates were somewhat greater (ca. 30%) than those observed for the PROBES studies in the late 70's and early 80's (Napp *et al.*, 1999). During 1998, the fate of organic material produced by primary production would be slightly different from 1997, although the amount of "new" production may be similar for both years. Smith and Vidal (1986) reported that the abundance and seasonal cycle of *Pseudocalanus* spp., one of the dominant species of copepods of the middle shelf, was greatly affected by temperature. Warmer water temperatures may have resulted in the faster development of *Pseudocalanus* spp., prior to the spring diatom bloom, and thus promoted an accelerated coupling to higher levels of pelagic food chain.

Table 5. Estimates of spring phytoplankton nitrate uptake in the southeast Bering Sea middle/outer shelf domain by the net change in integrated nitrate content of the mixed layer.

Year	Dates	Days	Outer Shelf (Sta 3-9)		Middle Shelf (Sta 12-17)	
			ΔNO_3 mg-at m ⁻² d ⁻¹	ΔC g C m ⁻² d ⁻¹	ΔNO_3 mg-at m ⁻² d ⁻¹	ΔC g C m ⁻² d ⁻¹
1979	26 Apr-27 May	31	30.3	1.82	31.1	1.87*
1980	23 Apr-24 May	31	21.8	1.31	30.0	1.80*
1981	13 Apr-14 May	31	11.6	0.69	25.1	1.50*
Mean			21.2	1.27	28.7	1.72
1997		~20			~38	2.3**
1998		~60			~35	2.1**

* Whittedge et al., 1986

** Whittedge (unpublished)

5. SUMMARY

1. Due to the anomalous physical conditions, there was an early sea ice related phytoplankton bloom over the middle shelf of the Bering Sea shelf during 1997 and apparently no water column bloom occurred until late May during 1998.
2. Nitrate uptake rates over the Bering Sea shelf in 1997 increased with depth due to the extension of the euphotic layer below the pycnocline. This deep nitrate uptake may be responsible for the apparent no change in Bering Sea zooplankton abundance and composition observed during 1997. However the inner shelf experienced significantly lower densities of adult euphausiids in and around the inner front region.
3. High ammonium uptake rates, high ammonium concentrations, and high sea surface temperatures may have stimulated the observed outbreak of a coccolithophorid blooms over the southeastern Bering Sea shelf during 1997.
4. During 1998, nitrate uptake rates were lower than expected from high nitrate concentration in the water column. Water column stability, high ammonium concentrations, and high water column temperature may have influenced the nitrate uptake rates.

5. According to nitrate depletion diagram analysis results, distinctively different atmospheric conditions during 1997 and 1998 may not dramatically affect the amount of “new” production. However, the different atmosphere conditions may have resulted in the obtained difference in transfer of production to higher trophic levels during 1997 and 1998. The early primary production event of 1997 preceded the increase in zooplankton numbers. The majority of this production, therefore, could have escaped zooplankton consumption and nourished the benthic community. The protracted growing season of 1998, however, allowed the zooplankton to more effectively graze the phytoplankton.

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